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Sattleria: a European genus of brachypterous alpine moths (Lepidoptera: Gelechiidae)

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CONTENTS

Synopsis 205
Introduction 205
Material and Methods 207
Abbreviations 208
Acknowledgements 209
The systematic position of *Sattleria* 209
Sattleria Povolný 210
Checklist of the species of *Sattleria* 214
Key to the species of *Sattleria* 215
References 240
Index 241

SYNOPSIS. The genus *Sattleria* Povolný (Gelechiinae, Gnorimoschemini), endemic to the alpine zone of European mountains, is revised. Eight species, including four newly described, are recognized as valid; one species is recalled from synonymy, one taxon reverts from subspecific to specific status, one subspecies is transferred to a different species and one synonym is newly established. Separate keys for males and females are provided, based on characters of the genitalia. Male and female moths and their genitalia are described and illustrated.

INTRODUCTION

In many parts of Europe the alpine zone was the last natural ecosystem almost undisturbed by man's activities and, as long as the mountains were remote and inaccessible, their unique flora and fauna could be considered relatively safe from destruction by mass tourism, intensive agriculture or industrial processes. Increasing recreational use of the mountains by a large, ever more affluent population, encouraged by commercial interests eager to exploit Europe's last touristic frontier, is now causing widespread overdevelopment and simultaneous destruction or fragmentation of sensitive natural habitats. Thus, numerous areas previously inaccessible to a wider public have been opened up to tourism through the construction of new roads, hotels, holiday chalets, ski lifts and pistes, cable cars and other facilities, and with the growing number of visitors such problems as the disposal of refuse add to the pressure on the environment. At the same time the agricultural sector's drive for greater profitability contributes through excessive application of fertilizers to reduced biodiversity even on remote alpine pastures, whilst long-range industrial air pollution appears to be responsible for dramatic die-back of alpine forests with resultant soil erosion (see, for example, Blab *et al.*, 1987: 170–177; Diem, 1988: 2–8).

Amongst the insects likely to be threatened by such degradation of their habitats a number of Lepidoptera species are particularly vulnerable, because their females are flightless and they are often confined to small disjunct colonies. An increased trend towards flightlessness with a more or less pronounced reduction of the wings has long been known to occur in the females of Lepidoptera inhabiting the alpine zone of high mountains in many parts of the world. Such abortion of flight and reduction of the flight organs as an apparent response to the ecological conditions in an extreme

environment is not confined to high altitude species but is also observed in many Lepidoptera endemic to small remote oceanic islands and in species which are active as adults during the cold season; the whole phenomenon is extensively reviewed by Sattler (1991).

In the European Alps examples of Lepidoptera species with wing reduction in the female sex are found in at least seven different families (Huemer & Sattler, 1989: 257) but the total number of species, which is in excess of 20, is still uncertain because several unresolved species-complexes are involved. One such complex is the gelechiid genus *Sattleria* Povolný (Gelechiinae: Gnorimoschemini), which is endemic to Europe and inhabits the higher mountains from the Pyrenees in the west to the Carpathians in the east in a number of disjunct populations. It is likely that, together with their habitats, many of its taxa are endangered; however, to obtain meaningful data for assessing the impact of adverse factors on the alpine ecosystem and its constituent parts, it is imperative first to understand the taxonomy of the organisms involved. It is therefore a purpose of this paper to elucidate the hitherto unresolved taxonomy of the known *Sattleria* populations and summarize the limited available ecological data.

When he proposed the genus *Sattleria*, Povolný (1965: 490–492) was ambivalent about the systematic status of the included taxa. He regarded the genus as monotypic, with *S. dzieduszyckii* (Nowicki) representing one variable species, but would not exclude the possibility that some of the more extreme morphologically separable forms might be distinct species. At the same time he dismissed *Gelechia pyrenaica* Petry as falling within the range of variation of *dzieduszyckii*, and subsequently synonymized it formally with the latter (Povolný, 1967: 175), although Petry had been emphatic that both were distinct. As Povolný's views had never been challenged it came as a surprise when, during a field trip by members of the BMNH Microlepidoptera Section (G. S. Robinson, K. Sattler & K. R. C. Tuck) in 1981, Petry's observations in the central Pyrenees were fully confirmed. On the slopes of Pic du Midi de Bigorre two *Sattleria* species, clearly separable in both sexes externally (Fig. 1) and by their genitalia, were found to fly together in the same biotope. In the light of these findings it was decided to reassess the taxonomic status of all *Sattleria* populations because it is not unreasonable to assume that, if two undisputed species occur side by side in the central Pyrenees, other morphologically separable forms elsewhere may also represent distinct species.

Preliminary results of our studies were presented at the Sixth Innsbrucker Lepidopterologengespräch, held on 20–21 October 1984 at the Tiroler Landesmuseum Ferdinandeum, where we produced evidence to support our view that *Sattleria* comprises a complex of several closely related but

Fig. 1 Males (left) and females (right) of two species of *Sattleria* from the Pyrenees: *S. arcuata* (top), *S. pyrenaica* (bottom).

morphologically distinguishable species. A second-hand report on our presentation prompted Povolný (1987) to pre-empt our planned publication by a hastily produced paper in which he reiterated his belief in *dzieduszyckii* as a single variable species. In essence he recognized several geographical forms, variously referred to as 'Rassenkomplex', 'Rassenkreis', 'Populationsgruppe' or subspecies, but emphasized that, for the time being, these are to be taken as representing merely statistical trends. At the same time he stated that it is impossible to assign individual moths of unknown geographic origin unambiguously to any of those subspecific groups. A key factor in his argument was the strong variation in size, coloration and genitalia structures he believed to have observed in his specimens from the Pyrenees; however, from his illustrated examples it is clear that he misinterpreted as intraspecific variation the differences between the widespread *S. pyrenaica* (Petry) and two geographically more restricted and hitherto undescribed species. Thus his colour figures, intended to demonstrate a remarkable range of variation in '*S. dzieduszyckii pyrenaica*', represent two males of *S. pyrenaica* (Petry) (figs 14, 15) from Pic du Midi and Mt Canigou respectively, flanked by *S. arcuata* sp. n. (fig. 13) from Pic du Midi and *S. angustispina* sp. n. (fig. 16) from Mt Canigou. It may have further misled Povolný that apparently he had transposed the genitalia of his specimens from Mt Canigou; the genitalia in text-fig. 12 belong to the moth in colour-fig. 16 and those in text-fig. 13 to the moth in colour-fig. 15, not the other way round as the accompanying label data would suggest.

Due to lack of material from several under-collected areas in the western Alps and mountains in Yugoslavia and Bulgaria there still remain some unresolved problems. Nevertheless, we believe to have shown in our study that *Sattleria* comprises several clear, morphologically distinguishable species.

MATERIAL AND METHODS

Our study of *Sattleria* is based on over 400 specimens (♂: ♀ ratio 6: 1), about 200 of which originated from various museums and private collections whilst a similar number was collected by us. All specimens recorded under 'Material examined' are in BMNH unless stated otherwise. The primary types of three of the seven previously described nominal taxa were examined, together with topotypical specimens of the other four, and most of the material recorded in earlier publications, usually as *Gelechia dzieduszyckii* Nowicki, was re-assessed, including several of the specimens illustrated or otherwise itemized by Povolný (1965; 1967; 1983; 1987). We were unable to trace any examples from Bulgaria (Rebel, 1903: 329) whilst the only known specimens from Montenegro (Rebel, 1913: 330) and Albania (Rebel & Zerny, 1931; 146), which belong to NM, Vienna, have not yet been returned by Povolný and were not examined.

We studied 117 genitalia slides (84 males, 33 females), most of which were specifically prepared for this work. The male genitalia were 'unrolled' in accordance with the technique previously described (Pitkin, 1986). Originally developed for the gelechiid genus *Mirificarma* Gozmány, this method also proved ideal for *Sattleria* males; without sacrificing any critical character it allows the two-dimensional display of all taxonomically important structures – a prerequisite for successful photomicrography. The advantages of the unrolling technique for interpreting complex genitalia structures are immediately obvious when our illustrations are compared with those of Povolný (1987, figs 1–13), which are based on conventional preparations of the 'entire', strongly three-dimensional genital armature.

As a result of a literature survey over 70 references to nominal taxa of *Sattleria* were traced; however, most of them are faunistic records or entries in catalogues and check-lists of little information value. Only a limited number of papers contain worthwhile biological observations (e.g., Burmann, 1954; 1977) or discuss taxonomic aspects (e.g. Povolný, 1965; 1967; 1987) and are recorded in the systematic part of our work.

In the past, collecting of *Sattleria* was mostly sporadic and only one lepidopterist ever made a special study (Burmann, 1954) in the course of which he accumulated appreciable series of specimens. Many of the mountains where *Sattleria* populations occur were rarely visited by microlepidopterists and minimal material exists in collections; for example, only one male each is known from Korab (Albania) and Durmitor (Montenegro) and very few specimens, all males, were ever collected in the Julijske Alpe (Slovenija) and Abruzzo (central Italy). Even in the much better explored Alps collecting was previously extremely difficult in the higher regions. Many suitable habitats could only be reached after long strenuous hikes and, as they usually lacked overnight shelter, field work was limited to just a few daytime hours, often further curtailed by the notoriously unpredictable weather conditions. Thus, like many

other Microlepidoptera of the alpine zone, *Sattleria* specimens are comparatively rare in collections, particularly the brachypterous females, and Povolny"s claim to have examined 'ample series' ('reichliche Serien') or 'extensive material' ('ausgedehntes Material') from 'all European mountain ranges, where [*Sattleria*] occurs' ('aus allen europäischen Gebirgen, wo sie vorkommt') (Povolný, 1965: 492; 1987: 85) is clearly exaggerated.

In recent times collecting and field studies have become very much easier, because more localities are now freely accessible by road or cable car and there are more facilities for spending the night in or near suitable habitats. We carried out field work in the central and eastern Pyrenees (K. S., 1981), southern Carpathians (L. M. P. & K. S., 1984) and Lechtaler Alpen (K. S., 1987) whilst unsuccessful searches for *Sattleria* were made in the eastern Alps (Raxalpe; K. S., 1985) and south-eastern Alps (Alpi Giulie/Julijske Alpe: Canin, Montasio, Mangrt; L. M. P. & K. S., 1987).

During the day, *Sattleria* males are occasionally flushed out of their hiding places, particularly in early morning and late afternoon, and can then be netted. Disturbed males fly only short distances, unless they are carried away by strong winds, and as they stay close to the ground they are sometimes difficult to see against the background of rocks and vegetation.

In suitable habitats with sparse vegetation and many flat stones a search of the ground can be most productive. Stones in the immediate vicinity of plant cushions can be turned over to expose specimens of both sexes, either sitting on the ground or on the underside of such stones.

As for other insects hidden in inaccessible substrates such as deep scree or dense vegetation, a beesmoker can be used successfully to drive *Sattleria* males and females out of hiding. This method is particularly effective on damp days when the smoke lingers on the ground. Smoke is usually produced from cartridges made of corrugated cardboard; however, locally available combustibles such as dry plant material or sheep dung can be substituted. During field work in the central Pyrenees on Pic du Midi de Bigorre a locally common lichen proved a most effective, long lasting fuel on damp days when it had the feel of good pipe tobacco, whilst on dry days it dried out quickly, becoming brittle and unsuitable. It is advantageous to impregnate one end of the cardboard cartridge with potassium nitrate for greater ease of lighting in windy weather. Care should be taken not to cause fires when emptying the beesmoker; in dry habitats it may be safer to restrict its use to damp days.

Both sexes of *Sattleria* respond to light (Burmann, 1954: 349; Klimesch, 1961: 650). The standard technique of running a mercury vapour light in front of a white sheet can therefore be employed but appears to produce only modest results, due to the limited motility of the moths. A night search between about midnight and 01.00 hrs with the aid of a Petromax paraffin lantern was found to be much more fruitful. A lantern placed on the ground during that time in a suitable habitat will attract the males in the near vicinity. The approaching moths can then be netted or collected directly into glass tubes, and every ten minutes or so the lantern is moved to a new location. In spite of a specific search no females were located with that method and few other Microlepidoptera were attracted at that time.

On occasions when a night search proved impractical or it was intended to sample different spots simultaneously, a Common trap was employed. This trap is equipped with a 6 watt actinic tube operated by a 12 volt car battery and charged with tetrachloroethane as a killing agent. It is specifically designed to collect the larger and small moths in separate compartments and thus prevent damage to the Microlepidoptera (Common, 1986). Only the males were caught in this trap, and inspections during its operation indicated that they were not usually attracted before midnight.

Rearing from the egg has not yet been tried and may be difficult if larvae overwinter twice as suggested by Burmann (1954: 350), but a search for larvae and pupae was found to be successful.

ABBREVIATIONS

BMNH	British Museum (Natural History), London, England.
BURM	Burmann collection, Innsbruck, Austria.
ETH	Eidgenössische Technische Hochschule, Zurich, Switzerland.
HUEM	Huemer collection, Innsbruck, Austria.
MCSN	Museo Civico di Storia Naturale, Milan, Italy.
MINGA	Muzeul de Istorie Naturala 'Grigore Antipa', Bucharest, Rumania.
MM	Moravske Museum, Brno, Czechoslovakia.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
NM	Naturhistorisches Museum, Vienna, Austria.
NMB	Naturhistorisches Museum, Basle, Switzerland.
TM	Természettudományi Muzéum, Budapest, Hungary.
WHIT	Whitebread collection, Magden, Switzerland.
ZI	Zoological Institute, Leningrad, U.S.S.R.

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The photographs were taken by the Photographic Unit, BMNH.

THE SYSTEMATIC POSITION OF *SATTLERIA*

S. dzieduszyckii (Nowicki), the type-species of *Sattleria* Povolný, has had a chequered history with regard to its generic position. Originally described in '*Gelechia* (*Anacampsis* HS.)', where it was placed next to *Acompsia maculosella* (Herrich-Schäffer) (Gelechiidae: Dichomerinae), it was subsequently transferred to *Doryphora* Heinemann (= *Xystophora* Wocke) and within that genus associated with species which are now accommodated in *Monochroa* Heinemann (Gelechiidae: Aristoteliinae) (Wocke, 1871: 298). Rebel (1901: 145) placed *dzieduszyckii* in *Gelechia* (subgenus *Gelechia*) amongst a group of species which were later separated as *Teleiopsis* Sattler, a position in which it was also retained by Meyrick (1925: 77). Following a revision of the collective genus *Gelechia*, *dzieduszyckii* was removed to the *Gnorimoschema* group (Gelechiinae: Gnorimoschemini) (Sattler, 1960: 69), where a separate genus, *Sattleria* Povolný, was eventually proposed for it.

Sattleria is established as monophyletic by several autapomorphies: in the male genitalia the presence of the usually forked posterior processes of the vinculum, and the anellus in the shape of a pair of perforated disks; in the female genitalia the presence of characteristic sternal pockets. A likely further autapomorphy is the reduction of the wings in the female sex.

Although it is universally accepted that *Sattleria* belongs to the Gelechiinae, tribe Gnorimoschemini, this has not yet been demonstrated beyond doubt. The main synapomorphy of the subfamily Gelechiinae is the division of the male abdominal segment 8 along the pleural line, which enables tergite and sternite to operate as independent covers for the genitalia. This arrangement separates the Gelechiinae from other subfamilies in which segment 8 forms a continuous ring into which the genitalia are usually withdrawn. In the *Sattleria* male the structure of segment 8 (Figs 48–50) clearly shows the gelechiine condition.

The Gelechiinae are currently divided into the tribes Gelechiini, Teleiodini and Gnorimoschemini. Whilst there appears to be agreement that most of the 40 genera united in the Gnorimoschemini form a monophyletic group, this has yet to be established and it is here suggested that the thorn-like signum bursae of the female is a synapomorphy of this tribe. Regrettably, in the *Sattleria* female the signum is secondarily lost and, until further synapomorphies are found, its gnorimoschemine status can only be deduced from overall similarities in conjunction with a specialized anellus character (see below) which *Sattleria* shares with a subgroup of undisputed Gnorimoschemini.

No classification of the Gnorimoschemini has ever been proposed, but an attempt was made by Povolný (1967) to express his views on the phylogenetic relationships of the genera within the tribe in a diagram, although it was not in the form of a cladogram. A recent idiosyncratic numerical analysis of phylogenetic relationships in Gnorimoschemini by Povolný & Sustek (1988) is less helpful because it does not provide clear results and merely demonstrates the unsuitability of the chosen technique for resolving such relationships. In Povolný's diagram of 1967 the Gnorimoschemini are divided into the gnorimoschemoid, scrobipalpuloid and scrobipalpoid branches, the last of which is subdivided into the scrobipalpoid, ephysterid and caryocolid groups of genera. The placement of *Sattleria* in the scrobipalpoid group next to *Scrobipalpopsis* Povolný and *Scrobipalpa* Janse was based primarily on similarities of the *Sattleria* fore wing pattern with that of *Scrobipalpopsis petasitis* (Pfaffenzeller) (Povolný, 1965: 490, text-fig.; 1967: 174); however, the mere presence of the three typical stigmata in both genera is irrelevant for establishing phylogenetic relationships, because it is a groundplan character of at least the ditrysian Lepidoptera, and no synapomorphies were found to confirm Povolný's view.

In contrast to Povolný it is here believed with Huemer (1988: 445) that *Sattleria* is closely related

to the so-called caryocolid genera *Agonochaetia* Povolný, *Pogochaetia* Staudinger, *Tila* Povolný, *Lutilabria* Povolný, *Klimeschiopsis* Povolný, *Caryocolum* Gregor & Povolný and *Cosmardia* Povolný, which are characterized morphologically by a reduction of the gnathos hook and development of sclerotized anellus structures in the male genitalia and biologically by the exclusive utilization of Caryophyllaceae as host-plants of the larvae (host-plants of *Agonochaetia* and *Lutilabria* unknown).

A hooked gnathos is probably a groundplan character of the Gelechiidae and is widespread in the Gnorimoschemini; its reduction in the caryocolid genera is here considered a synapomorphy of that group, and the well developed gnathos hook of *Sattleria* is a plesiomorphic character. In *Agonochaetia* (Fig. 65), *Pogochaetia*, *Tila* and *Caryocolum* (Fig. 64) the anellus is equipped with a pair of needle-like or peg-like sclerotizations, a structure unknown in other Gelechiidae. In the first three genera they are striking needles of considerable size, sometimes exceeding the aedeagus in length (Povolný, 1965: figs 8, 10, 11; 1974: figs 1–3; Sattler, 1968: fig. 11), whilst in *Caryocolum*, if present, they are short, peg-like and may bear a terminal seta (Huemer, 1988: figs 102, 123). The anellus of *Sattleria*, a pair of sclerotized disks with perforated centres (Fig. 66), an autapomorphy of this genus, is here interpreted as an extreme reduction of such structure and thus a synapomorphy with caryocolid genera.

Our view that *Sattleria* is closely related to caryocolid Gnorimoschemini is also supported by the host-plants of the larvae. Although, based on observations by Burmann (1954), it was assumed that *Sattleria* larvae were Saxifragaceae feeders, there is now increasing evidence that they live primarily on Caryophyllaceae, a plant family rarely utilized by Gelechiidae other than the caryocolid Gnorimoschemini. As far as can be ascertained from published and unpublished sources only five other gelechiid species can be associated with Caryophyllaceae: *Eulamprotes wilkella* (L.) on *Cerastium*; *Bryotropha figulella* (Staudinger) and *B. tachyptilella* (Rebel) possibly feeding on *Silene*; *Teleiodes myricariella* (Frey) normally feeding on Tamaricaceae but once reared on *Silene* (Huemer, pers. comm.); and *Scrobipalpa salinella* (Zeller) on Chenopodiaceae but occasionally found feeding on *Spergularia*.

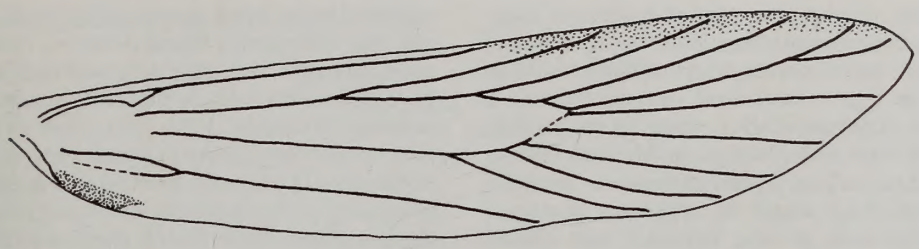
No study has been made to resolve the phylogeny within the caryocolid genera and it is not possible at this stage to identify the sister-group of *Sattleria*.

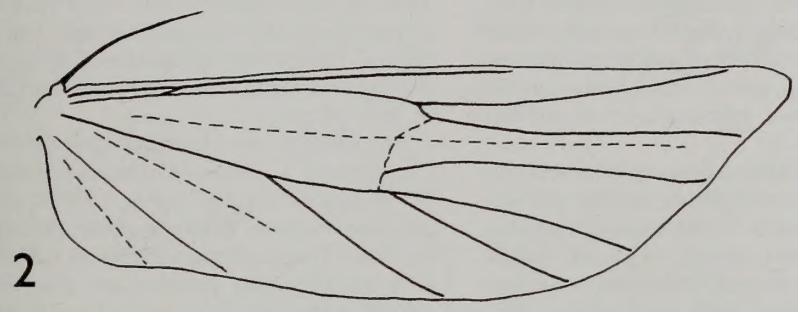
SATTLERIA Povolný

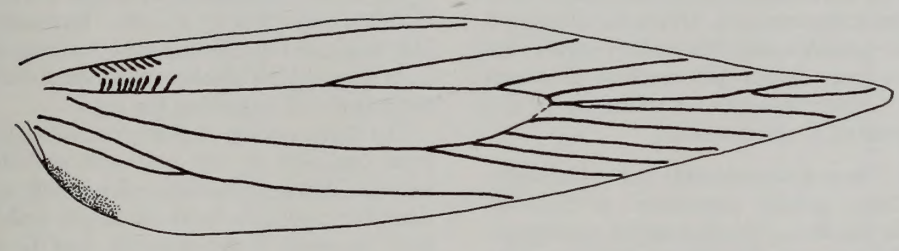
Sattleria Povolný, 1965: 490. Type-species: *Gelechia dzieduszyckii* Nowicki, 1864, by original designation and monotypy.

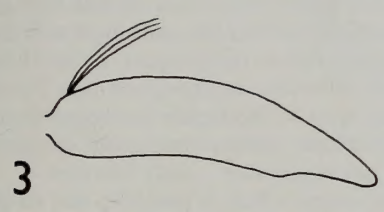
♂. 6.5–11.5 mm. Frons evenly convex. Ocellus present but small. Proboscis well developed, longer than labial palpus, squamose at base. Maxillary palpus with four segments, folded over base of proboscis. Labial palpus recurved, segment 3 acute, about as long as 2. Antenna two-thirds to three-quarters length of fore wing, scape without pecten. Fore wing broadest in distal half, length about 4.5–5 times greatest width; costa straight to weakly concave, weak indication of tornus. Coloration various shades of grey, with diffuse light transverse line extended between distal fifth of costa and tornus, stigmata black: short plical dash sometimes extended to base, discal often small but distinct, discocellular sagittate; usually complete row of marginal spots from distal fifth of costa around apex and along termen to tornus. Costa of fore wing (Fig. 2) with variably developed weak pterostigma between Sc and R5. Discal cell about three-fifths to two-thirds length of wing, discocellular vein oblique, more or less parallel to termen; R1 from middle, R2–R4+5 free from cell, free ends of R4 and R5 one-quarter to one-third length of common stalk; M1 close to or connate with R4+5; distance at base M1–M2 usually greater than M2–M3; distance CuA1–CuA2 variable, half to twice distance M3–CuA1. Hind wing (Fig. 2) about four-fifths length of fore wing, broad, costa almost straight, termen more or less straight, very weakly concave beneath apex. Sc+R1 to distal third of costa, R1 distinct between Rs and Sc; Rs and M1 separate, distance at base M1–M2 about twice M2–M3; M3 and CuA1 connate or on short stalk; CuA2 from about distal third of cell. ♀. 5.0–8.5 mm. As ♂ but antenna little shorter than fore wing. Fore wing (Fig. 3) broadly lanceolate, costa distinctly convex, no tornus, fringe very short. Coloration and markings similar to those of ♂ but discocellular stigma rarely sagittate, marginal spots always absent. All veins present and tubular as in ♂ but much closer together. Hind wing (Fig. 3) narrow, lanceolate, only about one-third length of fore wing, veins strongly reduced, not tubular; frenulum triple.

GENITALIA ♂ (Figs 27, 48–50). Tergite and sternite 8 separate, tergite narrower than sternite, posteriorly rounded; sternite broad, posteriorly rounded or with V-shaped median emargination; coremata absent. Uncus narrower than tegumen, distally more or less rounded. Gnathos with large









Figs 2, 3 Wing venation of *Sattleria melaleucella*. 2, ♂. 3, ♀ (different scale).

spiculate culcitula and strong, sharply pointed hook. Anterior margin of tegumen with broad emargination, pedunculi long. Valva usually slender, digitate; sacculus clearly separated, always shorter, shape variable. Posterior margin of vinculum with pair of characteristic, frequently forked, strongly sclerotized processes; saccus of moderate width, with more or less parallel margins. Anellus with pair of centrally perforated sclerotized disks. Aedeagus as long as or longer than tegumen, slender, straight; coecum hardly inflated, base sometimes splayed; ventral surface sometimes with median projection; apical arm with sclerotized hook, usually at right angles to longitudinal axis of aedeagus; ductus ejaculatorius enters dorsally near base.

GENITALIA ♀ (Fig. 28). Papilla analis longer than wide, unspecialised; apophysis posterior about three-quarters to four-fifths length of abdomen;

telescopic membranous part of ovipositor apparently without dorsal invagination or sac. Segment 8 dorsally membranous, sclerotizations confined to ventral and ventrolateral surface. Sternite 8 with pair of characteristic pockets, sternal surface medially often with conspicuous irregular folds or longitudinal ridges. Apophysis anterior rod-like, about one-third length of apophysis posterior; sclerotized area at base extended into ostium bursae, sometimes fused with posterior end of antrum; narrow, strongly sclerotized band from base to sternal pockets. Long tubular sclerotized antrum, more or less length of apophysis anterior. Membranous ductus bursae usually shorter than antrum, corpus bursae spherical or oval, without signum.

Ductus seminalis arising dorsally from anterior end of sclerotized antrum, short, without pseudobursa or bulla seminalis. Vestibulum with papilla. Canalis spiralis short, about length of canalis receptaculi; vesicula of moderate size; spermatheca (receptaculum seminis) with small lagena, utriculus about three to four times length of lagena, glandula receptaculi very long, filiform. Accessory glands with short ductus sebaceus, its half nearest junction of sacci sebacei an inflated reservoir; pair of narrow tubular sacci sebacei terminating in long filiform glandulae sebaceae. Oviductus communis inferior merged with anal tube shortly before anal opening to form cloaca. [Description of ductus seminalis – cloaca based on an examination of a single female of *S. melaleucella*.]

REMARKS. There is considerable individual variation in some genital characters of *Sattleria*, notably the saccus and the base of the aedeagus in the male, and an unusually high level of deformity was observed in the relatively small number of females examined. For example, two females of *melaleucella* have a strongly reduced apophysis anterior whilst the genitalia of one female of *angustispina* are strongly asymmetrical (Fig. 55). A barely discernible featureless vestigial signum was found in two individuals of *pyrenaica*; its presence is an indication that the loss of this organ in *Sattleria* is secondary but it is too strongly reduced to draw inferences as to its original shape.

BIOLOGY. Our knowledge of the biology of *Sattleria* is still sketchy, the only significant published observations being those made by Burmann (1954) in the Austrian Lechtaler Alpen. *Sattleria* species are restricted to the alpine zone of the European mountains where they can be found between 1500 m and 3500 m, although they usually occur upwards of 2000 m. Typical habitats are open slopes with coarse scree and sparse vegetation, but several species have also been observed in the dense grass of alpine pastures and amongst low growing *Rhododendron*. The freshly emerged moths, with their wings still undeveloped, have been observed in the early hours of the morning (Burmann, 1954: 348). Later in the day they usually hide deeper in scree, rock crevices or vegetation. In the early morning and at dusk, less frequently in the daytime, males are sometimes disturbed from their hiding places and fly short distances before settling again in a sheltered spot. They are relatively poor fliers but can run well and on rare occasions make short jumps. The brachypterous females are incapable of flying but can also run and, when disturbed, jump short distances of up to 50 mm.

According to our observations in the Pyrenees (*S. pyrenaica*, *S. arcuata*) and southern Carpathians (*S. dzieduszyckii*) the males have a period of particular activity between about midnight and 01.00 hrs. It seems logical to assume that this flight is in search of the females and that the latter should at the same time move from their hiding places to more exposed sites in order to await the males; however, no females were noticed by us during nocturnal searches. The courtship behaviour has never been observed, but a mating pair was found in the early afternoon under a stone, with the male half eaten by a spider. Burmann (1954: 349) suspected that a female he had seen walking from one plant to another in the afternoon was in the process of depositing her eggs.

The flight period of *Sattleria* can vary greatly from one year to the next and probably also between different localities, depending to a considerable extent on local conditions such as altitude, exposure to the elements, and the weather conditions in a given year. Adults examined by us were collected or bred between late June and mid-September; however, the main flight period appears to be mid-July to mid-August, unless these dates merely reflect the most popular time for entomological visits to the higher European mountains. Exceptionally, some reared adults did not emerge until late September – early October.

The ovum, which is probably laid singly or in small clusters on parts of the host-plant, has never been observed and the duration of the egg stage and the number of larval instars are unknown. It is also unknown whether the first instar larva mines, like the early instars of many other Gelechiidae including some *Caryocolum* species. Larvae have been found in July-August, living singly in a loosely spun silken tube that is often extended from the upper parts of the host-plant to the roots or nearby stones, where the larva seeks shelter when disturbed. The frass is deposited in a small heap outside the larval tube. Pupation takes place

Fig. 4 Distribution map of the species of *Sattleria*; 1, *S. arcuata*; 2, *S. pyrenaica*; 3, *S. angustispina*; 4, *S. breviramus*; 5, *S. melaleucella*; 6, *S. basistrigella basistrigella*; 7, *S. basistrigella triglavica*; 8, *S. styriaca*; 9, *S. dzieduszyckii*. Unconfirmed records are queried. Circles without numbers represent unidentified species. The dotted line represents the major mountain ranges of Europe.

in a dense cocoon that is spun under stones or amongst the host-plant and is often covered with grains of sand or particles of plant debris. As the larva may rest for some time in the cocoon before pupating, the length of the pupal stage is unknown, but it is unlikely to exceed two weeks.

It is not yet known how *Sattleria* overwinters. Based on his studies of *S. melaleucella* in the Lechtaler Alpen, Burmann (1954: 350; 1977: 146) assumed that overwintering takes place in the larval stage and that the presence of young and mature larvae together in July/August indicated that this might occur twice. Povolný (1987: 85, 86) claimed to have made similar observations on *S. dzieduszyckii* in the Czechoslovakian Tatry and in part supported Burmann's view but suggested that the larva might overwinter once or twice and even considered that the pupa might possibly lie over for the winter. The fact that freshly emerged adults can be found when the first plants are in bloom, soon after the snow has melted, indicates that at least some individuals overwinter in an advanced stage of development. Moreover, it could be argued that adults of *S. basistrigella*, which emerged in captivity as late as September/October, when their natural habitat at 2600 m may already have been snow-covered, would have remained as pupae in the wild. However, overwintering as a pupa is considered unlikely because all larvae reared to date have resulted in adults in the same season and there is as yet no evidence of a pupal diapause.

HOST-PLANTS

Caryophyllaceae: *Silene acaulis* (L.) Jacqu. – Switzerland, Zermatt (*Whitebread*) (*S. basistrigella*),
Cerastium latifolium L. – Austria, Rhätikon (*Huemer*) (*S. melaleucella*),
Cerastium uniflorum Clairv. – Austria, Lechtaler Alpen (*Huemer*) (*S. melaleucella*),
Moehringia sp. – Austria, Lechtaler Alpen (*Sattler*) (*S. melaleucella*) (a pupa found on this plant).
Saxifragaceae: *Saxifraga biflora* subsp. *macropetela* (Kern.) Rouay & Camus - Austria, Lechtaler Alpen (*Burmann*, 1954: 350; *Huemer*, *Sattler*) (*S. melaleucella*),
Saxifraga spp. – Czechoslovakia, Tatra mountains (Povolný, 1987: 88) (*S. dzieduszyckii*).

With one exception, the limited observations on the host-plants of *Sattleria* were made in the Alps and apply to only two species, *S. melaleucella* and *S. basistrigella*. The host-record for *S. dzieduszyckii* in the Tatra mountains, where Povolný (1987: 88) observed larvae on an unspecified *Saxifraga* species but failed to rear the moths, requires confirmation because we collected adults of the same species in the southern Carpathians in a spot where *Saxifraga* was so rare that other host-plants, probably Caryophyllaceae, must have been involved. Although *Saxifraga* species are the only host-plants of *Sattleria* recorded in the literature (Burmann, 1954, 1977; Povolný, 1987) there is now increasing evidence that the larvae are primarily Caryophyllaceae-feeders. Even in the Lechtaler Alpen, where Burmann found the larvae exclusively on *Saxifraga biflora* subsp. *macropetala*, further host-plants could be demonstrated when during an excursion to Muttekopf in mid-August 1987 (P. Huemer, K. & E. Sattler, I. Schatz) larvae were also discovered on *Cerastium uniflorum*, whilst a single pupa, from which a female later emerged, was found in a clump of *Moehringia*. Although *Sattleria* larvae clearly are oligophagous, i.e. they utilize more than one plant genus, in this instance even from two unrelated plant families, there is evidence that in some localities they may be specialized on just one plant genus or species. For example, Huemer (pers. comm.) observed the larvae of *S. melaleucella* in Rhätikon, Brandner Tal, exclusively on *Cerastium latifolium*, and a specific search on other plants, including species of *Saxifraga*, was unsuccessful. The suggestion that *Sattleria* larvae may be mining unspecified Compositae (Asteraceae) (Povolný, 1980: 204) is unsubstantiated and must be considered erroneous.

DISTRIBUTION (Fig. 4). Disjunct populations in higher European mountains. Pyrenees (Spain, Andorra, France), Alps (France, Switzerland, Germany, Austria, Italy, Yugoslavia), Appennino Abruzzese (Italy), Carpathians (Poland, Czechoslovakia, ? U.S.S.R.), Durmitor (Yugoslavia), Korab (Albania/Yugoslavia), Rila Planina (Bulgaria).

CHECKLIST OF THE SPECIES OF *SATTLERIA*

SATTLERIA Povolný, 1965
arcuata **sp. n.**
pyrenaica (Petry, 1904) **stat. rev.**
angustispina **sp. n.**
breviramus **sp. n.**
melaleucella (Constant, 1865) **sp. rev.**
fusca (Burmann, 1954) **syn. n.**
basistrigella basistrigella (Müller-Rutz, 1934) **stat. n.**
basistrigella triglavica Povolný, 1987, **stat. n.**
styriaca **sp. n.**
dzieduszyckii (Nowicki, 1864)
tatrica (Gregor & Povolný, 1955)

Key to the species of *Sattleria*

Males

1 Sacculus broad at base, abruptly tapered towards apex (Figs 33, 40, 41, 44, 47) 2
– Sacculus gradually tapered or base not broadened (Figs 29, 30, 32, 34–39, 43, 45, 46) 5

2 Secondary process of vinculum broad (Figs 40, 41, 44). Fore wing with distinct dark stripe along fold (Figs 12, 13, 15) 3
– Secondary process of vinculum narrow, sometimes filiform, difficult to discern (Figs 33, 47). Fore wing without distinct dark stripe along fold 4

3 Tapered apex of sacculus short; secondary process of vinculum angular or evenly rounded (Figs 40, 41) ..... ***basistrigella***
– Tapered apex of sacculus long, curved; secondary process of vinculum distinctly tapered (Fig. 44) ..... ***styriaca***

4 Primary process of vinculum about level with sacculus at apex; secondary process a distinct spine (Fig. 33) ..... ***angustispina***
– Primary process of vinculum not reaching base of sacculus; secondary process hair-like (Fig. 47) ..... ***breviramus***

5 Secondary process of vinculum broadly rounded (Figs 43, 45, 46) 6
– Secondary process of vinculum spine- or blade-like (Figs 29, 30, 32, 34–39) 7

6 Sacculus evenly tapered from base; secondary process of vinculum moderately broad, resembling a shark's fin (Figs 45, 46) ..... ***dzieduszyckii***
– Sacculus broadest at about distal third; secondary process of vinculum very broad (Fig. 43) ..... ***basistrigella triglavica***

7 Aedeagus traversed towards middle by broad arch; apical arm long, distinctly curved (Fig. 29) .. ***arcuata***
– Aedeagus not traversed by broad arch; apical arm straight or slightly curved, usually small (Figs 30–32, 35, 38, 39) 8

8 Aedeagus with median projection (Figs 35, 38); if projection small, secondary process of vinculum a triangular spine (Fig. 39) ..... ***melaleucella***
– Aedeagus without median projection; secondary process of vinculum a blade, apex often blunt (Figs 30–32) ..... ***pyrenaica***

Females

NOTE. The females of *breviramus* and *basistrigella triglavica* are unknown.

1 Pair of pockets in anterior half or middle of sternite 8 (Figs 51, 54, 56–59, 61) 2
– Pair of pockets in posterior half of sternite 8 (posterior edge of pocket at least two-thirds from anterior margin of sternite) (Figs 52, 53, 60, 62) 6
[If intermediate, treat as either state.]

2 Pockets at anterior end of sternite 8; inner edge of apophysis anterior approximately at right angle with sternite 8 (Fig. 54). ..... ***angustispina***
– Pockets at least slightly distant from anterior margin of sternite 8; inner edge of apophysis anterior forming even curve with sternite 8 (Figs 51, 56–59, 61) 3

3 Sclerotized area at base of apophysis anterior extended distinctly beyond sternal pockets towards middle of sternite; sclerotized antrum widely separated from sclerotized parts of sternite 8 (Fig. 51) ..... ***arcuata***
– Sclerotized area at base of apophysis anterior extended barely beyond sternal pockets; sclerotized antrum almost in contact with sclerotized parts of sternite 8 (Figs 56–59, 61) 4

4 Longitudinal ridges between pockets of sternite 8 distinct, approximated or partly fused (Fig. 59) ..... ***basistrigella basistrigella***
– Longitudinal ridges widely separated or indistinct (Figs 56–58, 61) 5

5 Longitudinal ridges between pockets of sternite 8 distinct, widely separated (Figs 56–58) .. ***melaleucella***
– Longitudinal ridges indistinct (Fig. 61) .... ***styriaca***

6 Sternite 8 with distinctly sclerotized medial ridges; antrum usually exceeding apophyses anteriores (Fig. 60) .. ***basistrigella basistrigella*** (southwestern form)
– Sternite 8 medially membranous; antrum not exceeding apophyses anteriores, usually shorter (Figs 52, 53, 62) 7

7 Sclerotized area at base of apophysis anterior broad, rounded, sometimes invaginated (Figs 52, 53) ..... ***pyrenaica***
– Base of apophysis anterior without broad, rounded sclerotized area (Fig. 62) ..... ***dzieduszyckii***

Sattleria arcuata sp. n.

(Figs 1, 4, 5, 17, 29, 48, 51)

[*Gelechia dzieduszyckii* Nowicki; Petry, 1904: 3–4. Misidentification.]

[*Sattleria dzieduszyckii pyrenaica* (Petry); Povolný, 1987: colour pl., fig. 13. Misidentification.]

♂, 7.7–11.0 mm. ♀, 5.5–6.8 mm. Labial palpus with dark apex. Fore wing (Figs 1, 5, 17) usually with large diffuse dark areas forming irregular indistinct transverse bands; without dark stripe along fold.

GENITALIA ♂ (Fig. 29). Sternite 8 usually rounded or barely emarginate posteriorly; rarely distinctly emarginate. Sacculus gradually swollen at base, not sharply broadened into lobe. Apex of primary process of vinculum almost level with apex of sacculus; sometimes with several setae scattered on outer surface; secondary process a narrow or broad-based spine, arising in basal quarter of

primary process; processes without serrated edges. Saccus usually parallel-sided, occasionally tapering slightly. Aedeagus without median projection; traversed towards middle by broad arch; apical arm a large hook. Base of aedeagus splayed, usually slightly.

GENITALIA ♀ (Fig. 51). Pair of narrow pockets in anterior half of sternite 8, at least slightly away from anterior margin. Pair of longitudinal ridges usually well separated. Pair of distinct sclerotized areas at base of apophyses anteriores projecting sharply beyond pockets of sternite 8. Inner edge of apophysis anterior forming even curve with sternite 8. Sclerotized antrum detached from base of, and extending beyond, apophyses anteriores; sclerotization at posterior end irregular, slightly convex or concave.

REMARKS. One of the largest species of *Sattleria*, *S. arcuata* is exceeded in size only by the largest specimens of *melaleucella*. It differs from the usually smaller *pyrenaica*, with which it occurs together, in the male by the posteriorly rounded rather than deeply emarginated sternite 8, the short, spine-like, smooth-edged secondary process of the vinculum, and the aedeagus with a strongly developed median arch and long, curved, apical arm. In the female genitalia *arcuata* is distinguished by the anterior rather than posterior position of the pockets in sternite 8, the sharply projecting sclerotized areas at the base of the apophyses anteriores, and the long detached sclerotized antrum.

BIOLOGY. Host-plant unknown. The adults occur in more or less heavily grazed alpine pasture and are found together with those of *S. pyrenaica*; however, whilst *arcuata* was only observed above 2100 m and was most frequent at about 2600–2700 m, *pyrenaica* was still common as low as 1600–1700 m. Flight period: July-August. Pic du Midi de Bigorre, the type-locality of *S. arcuata* and *S. pyrenaica*, was visited in 1981 by members of the BMNH Microlepidoptera Section. Although between 22 and 24 July it was still cold and there was much snow on the ground, the adults of *arcuata* were present in small numbers in snow-free spots, where some alpine plants were in flower. Following fresh heavy snowfall on 25 July the area was abandoned until 2 August, by which time most of the snow had melted and *arcuata* was found in quantity.

DISTRIBUTION (Fig. 4). Hautes-Pyrénées: Pic du Midi de Bigorre area (France).

MATERIAL EXAMINED (including 8 ♂, 3 ♀ genitalia preparations)

Holotype ♂, **France**: Hautes-Pryénées, Pic du Midi de Bigorre, 2650 m, 2.viii.1981 (*Sattler, Tuck & Robinson*) (genitalia slide no. 24678).

Paratypes. **France**: 1 ♂, Pyrénées, 2600 m, 2.viii.1927 (NM); 73 ♂, 8 ♀, Hautes-Pyrénées, Pic du Midi de Bigorre, 2400 m, 2650 m, 22.vii-4.viii.1981 (*Sattler, Tuck & Robinson*); 1 , Hautes-Pyrénées, Col du Tourmalet, 2150 m, 24.vii.1981 (*Sattler, Tuck & Robinson*); 1 , Hautes-Pyrénées, Gèdre 13.viii.1896 (MNHN).

Sattleria pyrenaica (Petry) stat. rev.

(Figs 1, 4, 6, 18, 28, 30–32, 49, 52, 53, 63)

Gelechia pyrenaica Petry, 1904: 3. LECTOTYPE ♂, FRANCE (Museum der Natur, Gotha, East Germany), here designated [examined].

Sattleria dzieduszyckii pyrenaica (Petry); Povolný, 1987: fig. 13, colour pl., figs 14, 15.

♂, 6.5–8.6 mm. ♀, 3.7–5.5 mm. Fore wing (Figs 1, 6, 18) without dark stripe along fold; usually without large dark areas, or weakly patterned.

GENITALIA ♂ (Figs 30–32). Sternite 8 emarginate posteriorly. Sacculus not broadened into lobe basally. Apex of primary process of vinculum almost level with apex of sacculus; without setae or with up to three setae; ventral edge of process sometimes slightly serrated. Secondary process of vinculum a blade with slightly serrated or uneven edge, arising between basal third and middle of primary process. Saccus usually slightly tapered. Aedeagus without median projection; never traversed by broad arch although narrow arch towards middle of aedeagus sometimes visible. Apical arm of aedeagus straight or slightly curved, usually small. Base of aedeagus usually strongly splayed.

GENITALIA ♀ (Figs 28, 52, 53, 63). Pair of broad pockets towards posterior margin of sternite 8; posterior edge of pocket at least two-thirds from anterior margin of sternite. Pair of sclerotized areas at base of apophyses anteriores with broad, rounded structure; distance between outer edges of these always greater (usually 1.5 times) than distance between outer edges of pockets. Antrum meeting base of, and shorter than, apophyses anteriores; sclerotization at posterior end often concave.

REMARKS. *S. pyrenaica*, the smallest species of the genus, is externally rather similar to *dzieduszyckii* but is easily distinguished in the male genitalia by the narrow, curved, rather than broadly rounded secondary process of the vinculum and the distinctly splayed base of the aedeagus. In the female both species share the posterior position of the

pockets in sternite 8 but in *pyrenaica* the sclerotized areas at the base of the apophyses anteriores are broad and rounded, and sometimes invaginated. Differences between *pyrenaica* and the other two *Sattleria* species known from the Pyrenees are discussed under *arcuata* and *angustispina* respectively.

A male from Pic du Midi de Bigorre, where *pyrenaica* occurs together with *arcuata*, shows some intermediate characters and is here interpreted as a hybrid between these two species. The almost unicolorous moth strongly resembles *pyrenaica*, and the abdominal sternite 8 is deeply emarginate posteriorly as in typical males of that species. In the genitalia (Fig. 27) the secondary process of the vinculum arises between the basal quarter and one-third of the primary process, as in *pyrenaica*, but is intermediate in shape; it is triangular and lacks the serrated edge characteristic of *pyrenaica*. As in that species, the aedeagus lacks a distinct median arch, whilst the apical arm, which resembles that of *arcuata*, is longer than that of *pyrenaica* and is distinctly curved.

G. pyrenaica was described from 13 male syntypes from Pic du Midi de Bigorre, eight of which have been examined.

GEOGRAPHICAL VARIATION. Specimens from the central Pyrenees, Andorra (males only) and Mt Canigou are remarkably uniform externally and in their genitalia. Two males from the Basses Alpes are here provisionally considered as an eastern form of *pyrenaica* although they differ in several characters from the main form in the Pyrenees. In the eastern form (Fig. 32) the secondary process of the vinculum is directed posteriad rather than laterad and is longer and less evenly curved than in the main form. At the same time the apical arm of the aedeagus is longer and slightly curved, resembling more that of *arcuata*, whilst the base of the aedeagus is only slightly splayed.

BIOLOGY. Host-plant unknown. The adults usually occur on more or less heavily grazed alpine pastures above 1600–1700 m. In all visited localities (central Pyrenees, Andorra, Mont Canigou) the males were attracted, like those of other *Sattleria* species (*S. arcuata* sp. n., *S. dzieduszyckii* (Nowicki)), between about midnight and 01.00 hrs to a Petromax paraffin hand lantern (see p. 000). On Pic du Midi de Bigorre and Mont Canigou some males were observed flying at dawn and dusk above low-growing *Rhododendron* shrub; in the latter locality they were also attracted to a Common trap placed in a small grove of 3–5 m tall pine trees. Above 2100 m on Pic du Midi de Bigorre *S. pyrenaica* was often found together with *S. arcuata* sp. n. The females were found by a careful search of the ground, usually hidden under stones, or were driven out of the vegetation with the aid of a beesmoker. Flight period: July-August.

DISTRIBUTION (Fig. 4). Pyrénées (France: Hautes-Pyrénées and Pyrénées Orientales; Andorra); Alps (France: Basses-Alpes).

MATERIAL EXAMINED

Main form (including 16 ♂, 5 ♀ genitalia preparations)

Lectotype ♂, **France**: [Haute-] Pyrénées, Pic du Midi de Bigorre, 2400–2700m, 24.vii.1901 (*Petry*) (Museum der Natur, Gotha).

France: 7 ♂ (paralectotypes), Pic du Midi de Bigorre, 2400–2700 m, 23–26.vii.1901 (*Petry*) (Museum der Natur, Gotha); 38 ♂, 13 ♀, Pic du Midi de Bigorre, 2400 m, 2650 m, 22.vii-4.viii.1981; 5 ♂, 1 ♀, Hautes-Pyrénées, Barèges – Col du Tourmalet 1600–1700 m, 25.vii.1981; 24 ♂, Pyrénées Orientales, Mt Canigou, 2200 m, 30, 31.vii.1981; 1 ♂, 2 ♀, Mt Canigou, 17.vii, 9.viii. 1894 (MINGA; MNHN, TM); 1 ♂, 1 ♀, [Pyrénées Orientales,] Lipaudère, 20.vii.1894 (MNHN). **Andorra**: 19 ♂, Coma del Forat, 2400 m, 28.vii. 1981.

Eastern form (including 2 ♂ genitalia preparations)

France: 2 ♂, [Basses-Alpes,] Chambeyron, 11.viii.1897 (MNHN).

Sattleria angustispina sp. n.

(Figs 4, 7, 19, 33, 50, 54, 55)

[*Sattleria dzieduszyckii* (Nowicki); Povolný, 1967: fig. 14. Misidentification.]

[*Sattleria dzieduszyckii pyrenaica* (Petry); Povolný, 1987: figs 12, 17 (partim), 24 (labelled in error as 25 in legend), colour pl., fig. 16. Misidentification.]

♂, 8.1–9.0 mm. ♀, 5.3–6.2 mm. Labial palpus with dark apex. Fore wing (Figs 7, 19) without dark stripe along fold; usually with irregular dark transverse bands.

GENITALIA ♂ (Figs 33, 50). Sternite 8 rounded posteriorly. Basal half of sacculus sharply broadened into lobe. Primary process of vinculum long, approaching apex of sacculus; secondary process a long narrow spine, arising in basal fifth of primary process; processes without serrated edges. Saccus tapered. Aedeagus with small median projection; apical arm small and straight. Base of aedeagus not noticeably splayed.

GENITALIA ♀ (Figs 54, 55). Pair of narrow pockets at anterior margin of sternite 8. Inner edge of apophysis anterior approximately forming right angle with sternite 8. Antrum slightly shorter than, or same length as, apophyses anteriores;

sclerotization at posterior end irregular, slightly convex.

REMARKS. *S. angustispina* is larger and much more variegated than *pyrenaica*, with which it occurs together on Mt Canigou. The male genitalia differ from those of all other *Sattleria* species in the long narrow secondary process of the vinculum, whilst the female is distinguished by the extremely anterior position of the pockets in sternite 8. One of the two females examined has deformed genitalia (Fig. 55).

BIOLOGY. Host-plant unknown. The few known adults have been collected at an altitude of about 2600 m. Flight period: July-August.

DISTRIBUTION (Fig. 4). Pyrénées Orientales, Mt Canigou (France).

MATERIAL EXAMINED (including 2 ♂, 2 ♀ genitalia preparations)

Holotype, ♂, **France**: [Pyrénées Orientales,] Mt Canigou, 17.vii.1894 (genitalia slide no. 67, LMP.; MINGA).

Paratypes. **France**: 2 ♂, 2 ♀, Mt Canigou, [1 ♂, 1 ♀] 2609 m, 15.vii-9.viii.1894 (MINGA; MNHN; TM).

Sattleria breviramus sp. n.

(Figs 4, 8, 47)

♂, 9.1 mm. Fore wing (Fig. 8) without distinct dark stripe along fold.

GENITALIA ♂ (Fig. 47). Sternite 8 unknown (abdomen not preserved in preparation). Sacculus basally broad, rounded, with narrow, abruptly tapered distal third. Primary process of vinculum short, not reaching base of sacculus; secondary process hair-like, situated at midpoint of primary process; processes without serrated edges. Saccus parallel-sided. Aedeagus without median projection; apical arm small and almost straight. Base of aedeagus not noticeably splayed.

GENITALIA. ♀ Unknown.

REMARKS. With the exceptionally short primary and thin hair-like secondary process of the vinculum *S. breviramus* is so striking that it warrants description although only the holotype male is known.

BIOLOGY. Host-plant unknown. Flight period: July.

DISTRIBUTION (Fig. 4). Alps (France: Alpes Maritimes).

MATERIAL EXAMINED (including 1 ♂ genitalia preparation)

Holotype ♂, **France**: Alpes Maritimes, [above St Martin-Vésubie,] 'Tre-Colpas, Madone de Fenestre', vii.1933 (*Praviel*) (genitalia slide no. 82, Gibeaux; MNHN).

Sattleria melaleucella (Constant) sp. rev.

(Figs 2, 4, 9–11, 20, 21, 34–39, 56–58, 66)

Gelechia melaleucella Constant, 1865: 197, pl. 7, figs 14 a, b. Syntypes, ♂, ♀, SWITZERLAND: Valais, Riffelberg or Riffelalp, vii [not traced]. [Synonymized with *Gelechia dzieduszyckii* Nowicki by Rebel, 1889: 315.]

Gelechia mariae Frey, 1867: 302. [Unavailable, nomen nudum.]

Gelechia dzieduszyckii Now. ssp. *fusca* Burmann, 1954: 345, pl. 18, figs 1–6, text-fig. 1. LECTOTYPE ♂, AUSTRIA (BURM), here designated [examined]. **Syn. n.**

[*Sattleria dzieduszyckii* (Nowicki); Povolný, 1965: figs 13, 16; 1967: fig. 32. Misidentifications.]

[*Gelechia dzieduszyckii* ssp. ?; Povolný, 1987: figs 5–8. Misidentification.]

[*Sattleria dzieduszyckii* ssp. ?; Povolný, 1987: figs 16 (partim), 20, 23 (labelled in error as 24 in legend), colour pl., figs 6, 9–11. Misidentification.]

♂, 7.3–11.6 mm. ♀, 5.8–8.5 mm. Labial palpus usually with dark apex. Fore wing (Figs 9–11, 20, 21) without dark stripe along fold; with or without irregular dark transverse bands.

GENITALIA ♂ (Figs 34–39). Sternite 8 with slight to deep emargination posteriorly. Sacculus slender, not broadened basally. Primary process of vinculum extending beyond base of sacculus and usually approaching apex of sacculus. Secondary process of vinculum a spine, usually narrow, occasionally triangular (south-eastern form C); arising at basal quarter to basal third of primary process; processes usually without serrated edges. Lateral margins of saccus concave, tapered or parallel. Aedeagus with large or (south-eastern form C) small median projection; apical arm small, straight or slightly curved. Base of aedeagus slightly to distinctly splayed.

GENITALIA ♀ (Figs 56–58). Pair of pockets, at least slightly conical, usually broad, in middle of sternite 8. Pair of distinct longitudinal ridges between pockets well separated, frequently with transverse ridges or fissures in between. Pair of sclerotized areas at base of apophyses anteriores projecting slightly or sloping gradually beyond pockets of sternite 8. Inner edge of apophysis anterior forming even curve with sternite 8. Antrum usually longer than anterior

apophyses; sclerotization at posterior end irregularly convex or produced in an inverted V-shape.

REMARKS. *S. melaleucella* resembles *S. arcuata* from the Pyrenees in its large size, variegated fore wings and the structure of the genitalia. The male differs from that of *arcuata* primarily in the aedeagus, which has a short, straight, rather than long, curved, apical arm and bears a distinct, median projection instead of the conspicuous arch characteristic of *arcuata*. A difference is also found in sternite 8, which is usually emarginated posteriorly rather than rounded as in *arcuata*. In the female genitalia the antrum tube of *melaleucella* almost makes contact with the extended bases of the apophyses anteriores whereas in *arcuata* the sclerotized antrum is separated from the sclerotized parts of sternite 8 by a wide membranous zone. The pockets of sternite 8 are usually broader in *melaleucella* and have a slightly more posterior position than those of *arcuata*; they are not sharply exceeded by the sclerotized areas at the base of the apophyses anteriores.

In Valais the distribution of *melaleucella* overlaps with that of *basistrigella*, but both species are easily distinguished externally by the dark stripe that accompanies the fold in the fore wing of *basistrigella*. The male genitalia of *melaleucella* differ from those of *basistrigella* by the narrow, evenly tapered sacculus and the narrow or triangular rather than broadly rounded or subrectangular secondary process of the vinculum. In the female genitalia of *melaleucella* the two longitudinal ridges between the pockets of sternite 8 are widely separated, whilst they more or less merge in *basistrigella*.

In the male there is considerable variation in the shape of sternite 8; the median emargination is shallow to deep and the two halves separated by it are posteriorly rounded to angular. The secondary process of the vinculum is subject to individual variation in length and width, and in one specimen from the Alpes-Maritimes (Fig. 37) it approaches that of *angustispina*. In this specimen the apical arm of the aedeagus is longer than usual, though not as long as in *arcuata*. In one female of *melaleucella* the antrum barely exceeds the apophyses anteriores; in two of the 12 females examined the genitalia are deformed. *G. melaleucella* was described from an unspecified number of specimens of both sexes, none of which have been traced. The lectotype designation by Viette (1951: 340) is invalid because the specimen he selected does not agree with Constant's original description or colour illustrations and thus could not have been part of the syntype series. Viette's 'lectotype' male, subsequently referred to as 'holotypic male' ('das holotypische Männchen') by Povolný (1983: 182) is in fact *basistrigella*.

G. dzieduszyckii fusca was described from a long series of specimens of both sexes, published as 'Typus ♂', 'Typus ♀' and 'Paratypen'. As no holotype was specified we formally designate as lectotype the specimen referred to as 'Typus ♂' and labelled as holotype by Burmann.

The name *Gelechia mariae* fails to conform to the *Int.-Code-zool.-Nom.*, Article 12, and thus is nomenclaturally unavailable. It was first proposed without a description, definition or indication (Frey, 1867: 302). The single specimen from Engadin, 'St. Maria', originally mentioned is still in the Frey collection (BMNH) and is a male of *S. melaleucella*.

GEOGRAPHICAL VARIATION. Specimens from the north-east of the range (Austria, eastern Switzerland), here termed form A (Figs 10, 21), usually have a more uniformly dark fore wing pattern than those from south-westerly localities (western Switzerland, Italy except Adamello mountains and Monte Baldo), here termed form B (Figs 9, 20), and also differ slightly in genital structure. Form A is usually larger, with a fore wing length of 9.8–11.6 mm (males), 7.3–8.5 mm (females), compared with 7.3–10.6 mm (males), 5.8–7.0 mm (females) in form B.

In the male of form A (Fig. 34) the secondary process of the vinculum is directed laterally, rather than posteriorly as in most specimens of form B, and tends to be broader (Figs 35–37). In the female of form A (Figs 57, 58) the posterior end of the sclerotized antrum is always a long inverted V, whereas in form B (Fig. 56) it varies from a short inverted V to irregularly rounded. The inverted V of form A ranges from 0.75–1.50 times the length of the tubular part of the antrum whilst in form B it is at most a little over half that length. The distance between the pockets of sternite 8 in the female is also variable and in form A is usually at least one-third the width of the entire segment (rarely less) whilst in the small sample of form B it never exceeds one-quarter that width.

Several of the specimens examined do not correspond exactly to either form. A female from Austria has the variegated fore wings of form B. A male from an intermediate locality, Engadin (Switzerland), has the fore wing pattern of form B but a secondary process of the vinculum resembling that of form A. Two males and one female from Savoie, the western end of the range of form B, also exhibit some intermediate characters. Their uniform but pale fore wing colour does not match that of either form whilst the secondary

process of the vinculum resembles that of form A; the associated female agrees with form A in the wing pattern and the distance between the pockets of sternite 8, but with form B in the sclerotization of the antrum. A male from the Alpes-Maritimes agrees with form B in genital characters but is intermediate in the wing pattern. In the males from the Appennino Abruzzese the apex of the secondary process of the vinculum tends to be blunter than in other *melaleucella*.

Whilst forms A and B only differ slightly from each other, specimens from the Adamello mountains and Monte Baldo, here termed form C, are more distinct. Form C falls within the size range of form B, which it also resembles in wing pattern, although it tends to have less distinct dark patches and sometimes is pale (Fig. 11). In some specimens of form C the traces of an irregular dark stripe are visible along the fold of the fore wing. In the male genitalia (Figs 38, 39) the secondary process of the vinculum is shorter and the primary process tends to be broader than in the other forms. In its direction the secondary process resembles that of form B but it tends to arise further from the base of the primary process than in either form A or B. The median projection of the aedeagus is much shorter than in other *melaleucella*. No females of form C were available for study. The differences between the three forms are insufficient to warrant giving them formal taxonomic status.

BIOLOGY. Host plants: *Cerastium latifolium* L., *C. uniflorum* Clairv., probably also *Moehringia* sp. (Caryophyllaceae); *Saxifraga biflora* subsp. *macropetala* (Kern.) Rouay & Camus (Saxifragaceae).

Larva fully grown about 14–15 mm long; head brown with darker speckles; prothoracic plate yellowish brown, thoracic legs blackish brown, lighter on inner side; abdomen light yellowish brown to loamy yellow with brown to reddish brown longitudinal lines, pinacula large, brown, setae short, light, anal plate and abdominal prolegs yellowish brown.

The lively larva inhabits a silken tube that is spun along parts of the host-plant, often extending from the tip of a shoot to the root or nearby stones towards which the larva quickly retreats when disturbed. Pupation takes place in a small cocoon that is frequently spun under a stone or sometimes under parts of the host-plant. In July/August young and mature larvae, pupae and adults can be found at the same time. (Burmann, 1954: 350; 1977: 146.) Flight period: July-mid-September.

S. melaleucella usually occurs on sparsely vegetated scree between 2000 and 3500 m; observations as low as 1600 m are exceptional. In the Lechtaler Alpen it is found in the summit regions where *Saxifraga biflora* subsp. *macropetala* is the dominant plant and also the main host-plant of the larva, although some larvae were found on *Cerastium uniflorum* and a single pupa amongst *Moehringia* (Burmann, 1954: 348; 1977: 143; Huemer & Sattler, pers. obs.). In the Brandner Valley, where it occurs above 2500 m on coarse scree with an *Androsace helvetica – Geum reptans* plant association, the host-plant of the larva is *Cerastium latifolium*; *Geum reptans* L. (Rosaceae), offered in captivity, was rejected (Huemer, pers. comm.).

DISTRIBUTION (Fig. 4). Alps (France: Alpes Maritimes to Austria: Lechtaler Alpen); Appennino Abruzzese. According to the literature also in the Allgäuer Alpen (Povolný, 1987: fig. 8, as *Gelechia dzieduszyckii* ssp. ?).

MATERIAL EXAMINED

Forms A and B (including 23 ♂, 12 ♀ genitalia preparations)

Lectotype ♂ (*fusca*), **Austria**: N. Tirol, [Lechtaler Alpen,] Muttekopf, 2700 m, 30.vii.1951 (*Burmann*) (BURM).

France: 1 ♂, [Alpes Maritimes,] Mt Mounier, 13.viii (MNHN); 2 ♂, [Savoie,] Col du Galibier, [1 ♂] 2500 m, viii.1974, 8.viii.1979 (BURM; MNHN); 1 ♀, Savoie, Col de l'Iseran, 2800–3000 m, 21.viii.1937 (MNHN). **Italy**: 1 ♂, [N. Italy,] 'Bozen'; 2 ♂, 'Monte Rosa', Mt Camoscio, 3, 4.viii.1906 (NM); 2 ♂, Abruzzo, Gran Sasso, 25.vii.1935 (MCSN); 2 ♂, Abruzzo, M Portella, 4.vii, 2.viii.1924 (MCSN); 1 ♂, Abruzzo, Mt Velino, 18.vii.1933 (MCSN). **Switzerland**: 1 ♂, [no data] (MNHN); 3 ♂, Valais (BMNH, MINGA); 1 ♂, V., near Montana, Mt Bonvin, 2900 m, 18.vii.1958 (WHIT); 1 ♂, [V., Turtmann Tal,] Gruben, vii.1904 (NMB); 2 ♂, [V.,] Trifthorn, [1 ♂] 3500 m, 7.viii.1920 (NMB); 1 ♂, [V.,] Mettelhorn, 30.vii.1934 (ETH); 4 ♂, [V.,] Zermatt; 1 ♂, 1 ♀, [V.,] Riffelberg, 26.vii.1928 (ETH); 3 ♂, 3 ♀, [V.,] Gornergrat, [1 ♂] 3000 m, 2.viii-13.ix.1934, 1937, 1969 (ETH; BURM; NMB; WHIT); 1 ♂, [V., Gamser Tal,] Gamsen ('Gamson') (MNHN); 1 ♂, [V.,] Simplon, 16.vii. 1912 (NM); 2 ♂, Simplon ('Sempione') (ETH); 7 ♂, 1 ♀, [Ticino,] 'Campolungo Pass', [1 ♂] 2324 m, 18–28.vii.1922, 1942, 1950 (NMB; ETH; BURM); 1 ♂, [Ticino,] Pizzo Molare, 11.viii. 1918 (NMB); 2 ♂, [Glarner Alpen,] Sardona ('Sardonna'), 19.vii.1901, 19.viii.1910 (NMB); 1 ♂, Engadin, Sta Maria. **Austria**: 2 ♂, 1 ♀, Vorarlberg, Brandner Tal, 'Wildberg', 2750 m, 22.viii.1984 (HUEM); 1 ♂, Brandner Tal, 'Tote Alpe', 2550, 14.viii.1985 (HUEM); 1 ♂, Brandner Tal, 'Sonnenlagant Alpe', 1600 m, 9.vii.1983

(HUEM); 18 ♂, 11 ♀ (*fusca* paralectotypes), N. Tirol, [Lechtaler Alpen,] Muttekopf, 2700 m, 30.vii.1951, 26.vii., 5.viii.1953 (*Burmann*) (BURM); 2 ♂, Muttekopf, 2650, 2700 m, 12.viii. 1987, 14.viii.1965 (BMNH; BURM); 1 ♀, Muttekopf, 2500 m, pupa on *Moehringia*, 12.viii.1987, moth emerged 18.viii.1987. No locality data: 7 ♂, 1 ♀ (BMNH; MINGA).

Form C (including 5 ♂ genitalia preparations)

Italy: 11 ♂, Adamello Mts, Mte Mandrone ('Mandron'), 2500, 2700, 2800 m, 30.vii-mid viii. 1958, 1964; 1 ♂, Mte Baldo, 'Telegrafo', 2150 m, mid vii.1969; (all BURM).

Sattleria basistrigella (Müller-Rutz) stat. n.

(Figs 4, 12–14, 22, 23, 40–43, 59, 60, 67)

Gelechia dzieduszykii [*sic*] f. *basistrigella* Müller-Rutz, 1934: 121, pl. 1, fig. 7.

♂, 8.2–10.0 mm. ♀, 5.5–7.0 mm. Labial palpus usually without dark apex. Fore wing (Figs 12–14, 22, 23) with dark stripe from base to one-third or two-fifths, along fold; males with diffuse irregular dark transverse band at two-thirds, sometimes faint, usually more pronounced at costa; some females with dark apex.

GENITALIA ♂ (Figs 40–43). Sternite 8 rounded posteriorly. Sacculus broad basally, widest at about middle to distal third, apex more or less abruptly tapered. Primary process of vinculum distally about level with apex of sacculus; secondary process very broad-based, large, subrectangular or more or less evenly rounded, edge sometimes uneven or weakly serrated. Saccus usually tapered. Aedeagus usually without, rarely with (south-western form), distinct median projection; apical arm short, straight or slightly curved. Base of aedeagus at most slightly splayed.

GENITALIA ♀ (Figs 59, 60). Pair of narrow pockets in anterior or (south-western form) posterior half of sternite 8, with posterior edge of pocket up to two-thirds from anterior margin of sternite. Pockets at least slightly distant from anterior margin of sternite. Pair of distinct, irregular longitudinal ridges between pockets close together. Pair of sclerotized areas, at base of apophyses anteriores, projecting slightly or sloping gradually beyond pockets of sternite 8. Inner edge of apophysis anterior forming even curve with sternite 8. Antrum usually barely longer than apophyses anteriores; sclerotization at posterior end irregular.

REMARKS. *S. basistrigella* is distinguished externally from all *Sattleria* species except *styriaca* by the distinct continuous black stripe along the basal two-thirds of the fore wing fold. This stripe is an extension of the plical stigma which, in other species, is streak-like but not extended to the wing base. The male genitalia of *basistrigella* are distinguished from those of other species either by the medially broad rather than evenly tapered sacculus or the broad secondary process of the vinculum. Differences from *melaleucella*, with which *basistrigella* occurs together in some localities, and *styriaca* are discussed under those species.

GEOGRAPHIC VARIATION. Specimens from the south-western and eastern extremes of the range tend to be slightly smaller than those of the main form. In the male genitalia they resemble each other in the basal swelling of the sacculus, which is smoothly rounded whereas in the main form it is spinose and often irregularly rounded, and the secondary process of the vinculum, which is larger and more rounded than that of the main form. The south-western form (Savoie) differs from other *basistrigella* in the presence of a median projection on the aedeagus. In the female of the south-western form the pockets of sternite 8 are broader and inserted more posteriorly than in the main form; the female of the eastern form *(basistrigella triglavica)* is still unknown.

The name *triglavica* Povolný, originally proposed as a subspecies of *dzieduszyckii*, is here retained for the eastern form of *basistrigella*, although there are only slight differences between this and the south-western form.

BIOLOGY. Host-plant: *Silene acaulis* (L.) Jacqu. (Caryophyllaceae). The larva (Fig. 67), which is similar to that of *melaleucella*, was observed in July, living in a silken tube on the host-plant (Whitebread, pers. comm.). Flight period: July-August. Adults reared by Whitebread from larvae collected on 23.vii.1984 emerged 29.ix-9.x.1984, at a time when their natural habitat may already have been snow-covered. *S. basistrigella* occurs from about 2400 m to above 3000 m.

DISTRIBUTION (Fig. 4). Alps (France: Savoie, to Yugoslavia: Julijske Alpe).

Sattleria basistrigella basistrigella (Müller-Rutz)

(Figs 4, 12, 13, 22, 23, 40, 41, 59, 60, 67)

Gelechia dzieduszykii [*sic*] f. *basistrigella* Müller-Rutz, 1934: 121, pl. 1, fig. 7. LECTOTYPE ♂, SWITZERLAND (ETH), here designated [examined].

[*Gelechia melaleucella* Constant; Viette, 1951: 340. Misidentification.]

'*Gelechia*' *dzieduszyckii* Now. v. *basistrigalis* M.R.; Klimesch, 1963: 13. [Incorrect subsequent spelling of *basistrigella* Müller-Rutz.]

[*Gelechia dzieduszyckii* sp. ?; Povolný, 1987: fig. 10. Misidentification.]

[*Sattleria dzieduszyckii* ssp. ?; Povolný, 1987: fig. 16 (partim), colour pl., fig. 7. Misidentification.]

♂, ♀, (Figs 12, 13, 59, 60). As described on p. 221.

GENITALIA ♂ (Figs 40, 41). As described on p. 221.

GENITALIA ♀ (Figs 59, 60). As described on p. 221.

REMARKS. *S. b. basistrigella* was described from an unspecified number of males and females from Gornergrat and nearby Trift. We have examined five males of the type series from the collections of the ETH and NMB. Six further specimens in the ETH bearing 'Type' or 'Cotype' labels cannot be regarded as type material since they bear dates of collection subsequent to the original description or are from a different locality.

DISTRIBUTION (Fig. 4). Alps (France: Savoie, Switzerland, Italy).

MATERIAL EXAMINED

Main form (including 9 ♂, 4 ♀ genitalia preparations)

Lectotype ♂, **Switzerland**: [Valais,] Gornergrat, 19.vii.1931 (*Weber*) (genitalia slide no. 1259; ETH).

Switzerland: 4 ♂, 2 ♀, Valais (BMNH; MNHN); 1 ♂, V., Grand St Bernard, 2472 m, 5.viii.1980 (WHIT); 2 ♂, 2 ♀, V., [Zermatt,] Schwarzsee, [2 ♂, 2 ♀] 2580 m, 9.viii.1932, [e.l.] 29.ix.1984, [e.l.] 6, 9.x.1984 (WHIT; ETH); 5 ♂, 3 ♀, V., Zermatt, Trift, [4 ♂] 2700, 2800 m, 18.vii-2.viii.1934, 1981, 1982 (WHIT; ETH; NMB; BURM); 3 ♂ (paralectotypes), Trift, 23.vii.1928, 7.viii.1932 (*Weber & Müller-Rutz*) (ETH; NMB); 2 ♂, 2 ♀, Zermatt, 27.vii.1934 (ETH); 1 ♂, [near Zermatt,] Täsch, 2850 m, 2.viii.1984 (WHIT); 1 ♂ (paralectotype) [V.,] Gornergrat, 31.vii.1932 (*Müller-Rutz*) (NMB); 6 ♂, 2 ♀, Gornergrat, 19–30.vii.1925, 1934 (NMB; ETH; MNHN); 1 ♂, V., Binn, 2–7.viii.1908; 1 ♀, V., 'Col du Pigne', 3130 m, 23.vii.1983 (WHIT). **Italy**: 1 ♂, [N. Italy,] 'Bozen'; 1 ♂, Carbonin ('Schluderbach') (NM). No locality data: 5 ♂, 14, 27.vii.1905 (BMNH; MNHN; TM).

South-western form (including 3 ♂, 2 ♀ genitalia preparations)

France: 8 ♂, Savoie, Bonneval-sur-Arc, 24.vii, 14.viii.1912 (MNHN); 2 ♀, [S.], Col d'Iseran, [1 ♀] 2900 m, 21.viii.1937, 24.viii.1974 (MNHN); 1 ♂, S., Val-d'Isère, 30.vii.1895 (MNHN).

Sattleria basistrigella triglavica (Povolný) stat. n.

(Figs 4, 14, 42, 43)

Sattleria dzieduszyckii triglavica Povolný, 1987: 91, colour pl., figs 4, 5. Holotype ♂, YUGOSLAVIA: 'Krain', Triglav, 2400 m, mid vii.1927 (Povolný collection, Brno) [not examined].

Gelechia dzieduszyckii triglavica Povolný, 1987: figs 3, 4.

♂. Dark stripe on fore wing (Fig. 14) and diffuse irregular transverse band fainter than in other *basistrigella*.

GENITALIA ♂ (Figs 42, 43). Sacculus less swollen than in other *basistrigella*. Secondary process of vinculum a broad-based rounded lobe situated at base of primary process. Saccus parallel-sided. Aedeagus with, at most, indistinct median projection.

GENITALIA. ♀ Unknown.

REMARKS. Povolný believed all *Sattleria* specimens to represent just one variable species and consequently described *triglavica* as a subspecies of *dzieduszyckii*. Our study has shown that it is conspecific with *basistrigella* rather than *dzieduszyckii* sensu stricto and is particularly similar to the south-western form (Savoie) of that species. We have been unable to examine the holotype of *triglavica* but have studied other specimens from the type-locality Triglav. The paratypes from Steiermark are not conspecific with *basistrigella* and represent *S. styriaca* sp. n.

The following type material of *triglavica* was recorded in the original description:

Holotype ♂, 1 paratype ♂, Krain, Triglav, 2400 m, mid-vii.1927 (*unspecified collector*). One of the two moths was illustrated by Povolný (1987: colour pl., fig. 4) together with the genitalia of the paratype (text-fig. 3). [Not examined.]

Paratype ♂, Montenegro, Durmitor, 2000 m, 2.viii. (*Penther*). The moth and genitalia were illustrated by Povolný (1987: colour pl., fig. 5; text-fig. 4). [Not examined.]

Paratype ♂, Albania, Korab, 28–31.vii.1918 (*Albania-Expedition, Mus. Vienna*). [Not examined.]

Paratype ♂, Steiermark, Dachsteingebiet, 2300 m, 24.vii.1923 (*collector unknown*) (genitalia slide no. 1836, NM). [Examined.] Neither the moth nor the associated genitalia preparation are labelled as 'paratype'; however, the latter is identified as 'ssp. *triglavica*' on Povolný's slide label. Our examination has shown that this specimen is not conspecific with *triglavica* but represents *S. styriaca* sp. n.

[? Paratype] ♀, Steiermark, Seetaler Alpen,

Zirbitzkogel, 2200 m, Z. ['Zucht', indicates reared specimen] 28.vii.1911 (*collector unknown*) (genitalia slide no. 1837, NM). [Examined.] This specimen was omitted from Povolný's list of material examined on p. 92, but was recorded on p. 97 (legend to text-fig. 19). Although the altitude is there given as 2300 m and the date of capture as 22.vii., the genitalia are clearly those illustrated in text-fig. 19 and in earlier papers (Povolný, 1965: fig. 15; 1967: fig. 31); they represent *S. styriaca* sp. n.

The depository of the type material was not specified in the original description; however, according to Lödl (in lit., 8.iv.1987), Povolný claims the first four specimens to be his property, although there is evidence in the literature (Rebel, 1913: 330; Rebel & Zerny, 1931: 146) that at least those from Montenegro and Albania originated from the NM, Vienna.

BIOLOGY. Host-plant unknown. Flight period: July-August.

DISTRIBUTION (Fig. 4). Julijske Alpe (northwestern Yugoslavia). Also recorded from southwestern Yugoslavia (Montenegro, Durmitor) (Povolný, 1987: 92, text-fig. 4; colour pl., fig. 5) and Albania (Korab) (Povolný, 1987: 92); however, we were unable to examine specimens from those localities and thus cannot confirm these records.

MATERIAL EXAMINED (including 2 ♂ genitalia preparations)

Yugoslavia: 2 ♂, Slovenija ('Carniola'), Triglav, 26.vii, 3.viii.1929 (*Kautz*) (NM).

Sattleria styriaca sp. n.

(Figs 4, 15, 24, 44, 61)

[*Sattleria dzieduszyckii* (Nowicki); Povolný, 1965: fig. 15; 1967: fig. 31. Misidentifications.]

[*Sattleria dzieduszyckii* ssp. ?; Povolný, 1987: fig. 11. Misidentification.]

[*Sattleria dzieduszyckii triglavica* Povolný; Povolný, 1987: fig. 19. Misidentification.]

♂, 10.0–10.8 mm. ♀, 7.6 mm. Labial palpus with dark apex. Fore wing (Figs 15, 24) with dark stripe from base to one-third or two-fifths, along fold; usually with diffuse irregular dark transverse band at two-thirds (males), sometimes faint, or (females) near apex.

GENITALIA ♂ (Fig. 44). Sternite 8 rounded posteriorly. Sacculus composed of broad, blunt-ended basal section and narrow, curved, gently tapered distal part. Primary process of vinculum short, apex about level with blunt end of sacculus; secondary process broad-based, posteriorly tapered lobe arising at base of primary process; processes smooth, without serrated edges. Saccus distinctly tapered. Aedeagus with tiny median projection; apical arm small and more or less straight. Base of aedeagus scarcely splayed.

GENITALIA ♀ (Fig. 61). Pair of broad, rounded pockets near but not directly at anterior margin of sternite 8. Pair of longitudinal ridges between pockets of sternite 8 indistinct. Pair of sclerotized areas, at base of apophyses anteriores, projecting slightly or sloping gradually beyond pockets of sternite 8. Inner edge of apophysis anterior forming even curve with sternite 8. Antrum about as long as apophyses anteriores; sclerotization at posterior end irregular, barely convex.

REMARKS. Externally *S. styriaca* resembles *basistrigella* in the presence of a black continuous plical stripe on the fore wing. It differs in the male genitalia by the characteristic sacculus with a long, strongly curved apical portion and by the broadly based, posteriorly tapered secondary process of the vinculum. The female genitalia are distinguished from those of some forms of *basistrigella* by the anterior position of the sternal pockets and the absence of distinctly sclerotized longtitudinal folds between them. In the main form of *basistrigella* the sternal pockets are in a similarly anterior position but are smaller and more pointed.

BIOLOGY. Host-plant unknown. The few adults known to date have been collected at an altitude of about 2200 – 2300 m. Flight period: late July-beginning of August.

DISTRIBUTION (Fig. 4). Alps (Austria: Steiermark).

MATERIAL EXAMINED (including 3 ♂, 2 ♀ genitalia preparations)

Holotype ♀, **Austria**: Steiermark, Seetaler Alpen, 'Zirbitzkogel', 2200 m, 1.viii.1911 (genitalia slide no. 11240; NM).

Paratypes. **Austria**: 2 ♂, 1 ♀, Steiermark, Seetaler Alpen, 'Zirbitzkogel', 2300 m, 22.vii.1911 (NM); 1 ♂, Steiermark, Dachstein area, 2300 m, 24.vii.1923 (NM). No locality data: 1 ♂ (NM).

Sattleria dzieduszyckii (Nowicki)

(Figs 4, 16, 25, 26, 45, 46, 62)

Gelechia (*Anacampsis* HS) *dzieduszyckii* Nowicki, 1864: 20, fig. 4. Syntypes, ♂, POLAND: Tatry [,near Zakopane]: Bobrowiec; Kopa Magury ('Magóra'); Kosista ('Koszysta'); Woloszyn; viii (*Nowicki*) [not traced].

Gelechia dzieduszyckii tatrica Gregor & Povolný, 1955: 120, 127, phot. 2, fig. 4. Holotype ♂, CZECHOSLOVAKIA: Vysoké Tatry, Rysy, 2000 m, 23.vii.1951 (*Miller*) (MM) [not examined]. [Synonymized by Povolný, 1987: 91.]

♂, 6.9–8.8 mm. ♀, 4.9–5.6 mm. Fore wing (Figs 16, 25, 26) usually uniform, without large dark areas, some males with diffuse dark spot at two-thirds, mainly at costa; plical stigma sometimes indistinctly extended towards wing base.

GENITALIA ♂ (Figs 45, 46). Sternite 8 emarginate posteriorly. Sacculus evenly tapered, basal part not conspicuously broadened. Primary processes of vinculum almost level distally with apex of sacculus, ventral edge slightly serrated, except apically; secondary process arising at slight distance from base of primary process, consisting of a moderately broad, rounded lobe resembling a shark's fin, with uneven or slightly serrated edge. Saccus with parallel margins or slightly tapered. Aedeagus with weak median projection; apical arm short, almost straight to moderately curved; base rarely distinctly splayed.

GENITALIA ♀ (Fig. 62). Pair of broad pockets in posterior half of sternite 8; posterior edge of pocket at least two-thirds from anterior end of sternite. Pair of sclerotized areas at base of apophyses anteriores without broad, rounded structure; distance between outer edges of these usually less than or equal to distance between outer edges of pockets, occasionally slightly greater. Inner edge of apophysis anterior forming even curve with sternite 8. Antrum barely shorter than apophyses anteriores; sclerotization at posterior end irregularly convex.

REMARKS. Externally *dzieduszyckii* closely resembles *pyrenaica* in size, coloration and wing pattern, but is easily distinguished by the male and female genitalia; differences are discussed under *pyrenaica*. In the fore wing of *dzieduszyckii* the plical streak is sometimes extended towards the wing base as in *basistrigella*, but it is less pronounced than in the latter. The male genitalia of *dzieduszyckii* are distinguished from those of most other *Sattleria* species by the broadly rounded secondary process of the vinculum; they differ from those of *basistrigella*, which sometimes have a similar though distinctly broader rounded process, by the evenly tapered sacculus. The female genitalia of *dzieduszyckii* are distinguished from those of all *Sattleria* species, except *pyrenaica*, by the posterior position of the broad pockets in sternite 8. The differences from *pyrenaica* are discussed under that species.

In the original description of *dzieduszyckii*, Nowicki referred to both males and females but later admitted that he had been mistaken and in fact had only seen males (Rebel, 1889: 315). According to Rebel there should be type-specimens in NM, Vienna; however, amongst other *dzieduszyckii* from the Tatra mountains we located in that collection only one male originating from Nowicki. This specimen is dated 1865, too late for it to have syntype status.

G. dzieduszyckii tatrica was described from the holotype and five paratypes, all males, from Vysoké Tatry. When proposing this subspecies, Gregor & Povolný separated it from the populations of the Alps but overlooked the fact that the Tatra mountains are the type-locality of the nominate subspecies *d. dzieduszyckii*.

BIOLOGY. Host-plant not known with certainty. In the north-western Carpathians (Tatry), Povolný (1987: 88) observed larvae in silken tubes on *Saxifraga* species (Saxifragaceae) but failed to rear the adults. In a locality in the southern Carpathians (Bucegi), where we found the adults in late July – early August 1984, *Saxifraga* was so rare that other host-plants such as *Silene acaulis* or *Cerastium* (Caryophyllaceae) were probably involved. The larva has not yet been described but is likely to resemble that of *melaleucella* and have a similar biology. Flight period: late June – mid-August, annually variable.

S. dzieduszyckii occurs on alpine pastures or sparsely vegetated ground and scree between about 1800 and 2600 m. In the Bucegi mountains (southern Carpathians), on a plateau at about 2000 m, we observed the adults in pasture with dense, heavily grazed grass and some alpine vegetation.

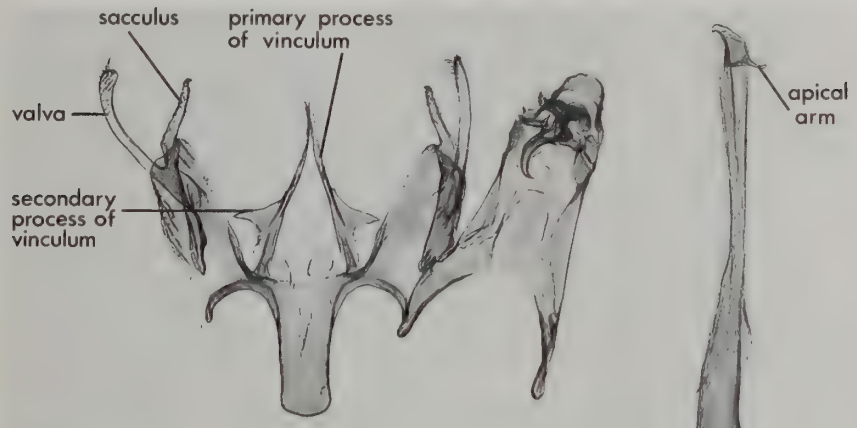
DISTRIBUTION (Fig. 4). North-western Carpathians (Polish and Czechoslovakian Tatry), southern Carpathians (Rumanian Carpatii Meridionali). Included by Piskunov (1981: 689) amongst the Gelechiidae of the European U.S.S.R. as occurring in the Carpathians. Although no detailed locality was recorded, the presence of *dzieduszyckii* in the Ukrainian Carpathians with their highest mountains just above 2000 m is not impossible. A record for 'Hungary' (Pável & Uhryk, 1896: 69, as *melaleucella*) which, in its present borders, lacks mountains high enough to have an alpine zone, dates back to the time of the Austro-Hungarian empire and applies to the north-western Carpathians. Also recorded from Bulgaria (Rila Planina) (Rebel, 1903: 329), but we were unable to trace voucher specimens and the status of that population remains uncertain. All previous records of *dzieduszyckii* from the Pyrenees, Alps and Appennino apply to other *Sattleria* species.

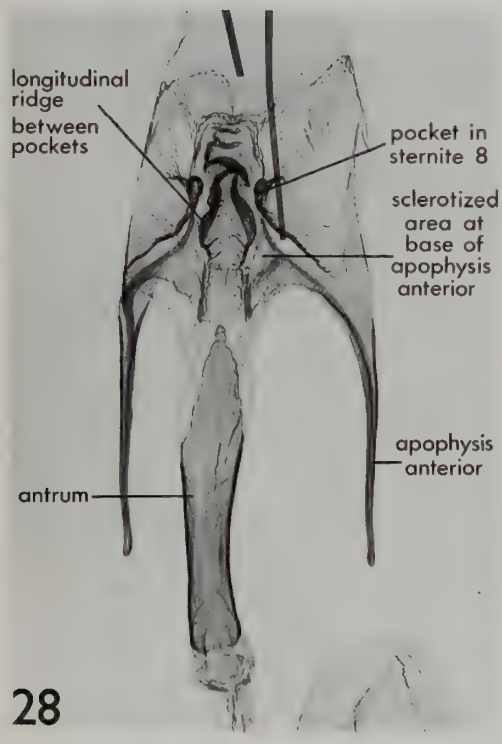
Figs 5–10 Wings of *Sattleria* males. 5, *S. arcuata*. 6, *S. pyrenaica*. 7, *S. angustispina*. 8, *S. breviramus*. 9, *S. melaleucella* (form B, Switzerland: Valais). 10, *S. melaleucella* (form A, Austria: Lechtaler Alpen).

Figs 11–16 Wings of *Sattleria* males. 11, *S. melaleucella* (form C). 12, *S. basistrigella basistrigella* (main form). 13, *S. basistrigella basistrigella* (south-western form). 14, *S. basistrigella triglavica*. 15, *S. styriaca*. 16, *S. dzieduszyckii*, Tatry.

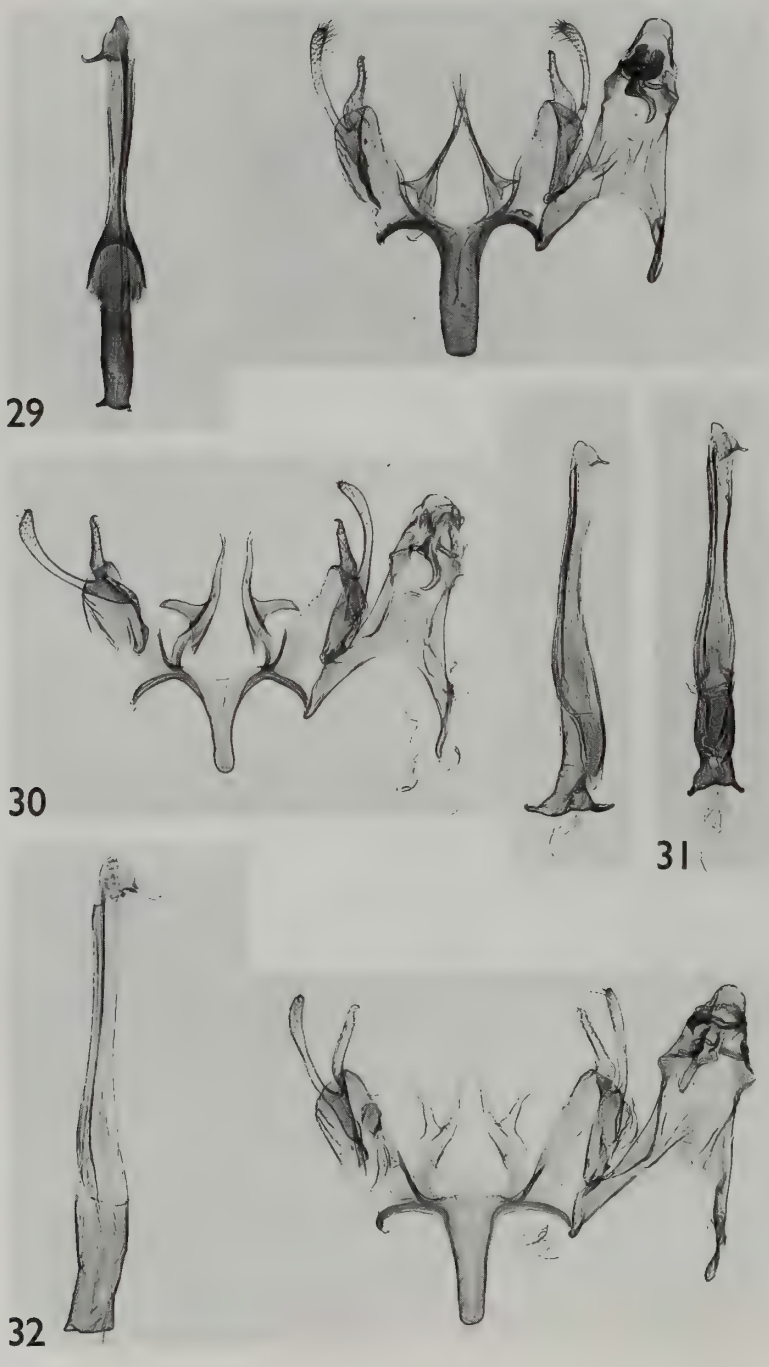
Figs 17–22 *Sattleria* females. 17, *S. arcuata*. 18, *S. pyrenaica*. 19, *S. angustispina*. 20, *S. melaleucella* (form B, Switzerland: Valais). 21, *S. melaleucella* (form A, Austria: Lechtaler Alpen). 22, *S. basistrigella basistrigella* (main form).

Figs 23–26 *Sattleria* females. 23, *S. basistrigella basistrigella* (south-western form). 24, *S. styriaca*. 25, *S. dzieduszyckii*, Tatry. 26, *S. dzieduszyckii*, southern Carpathians.



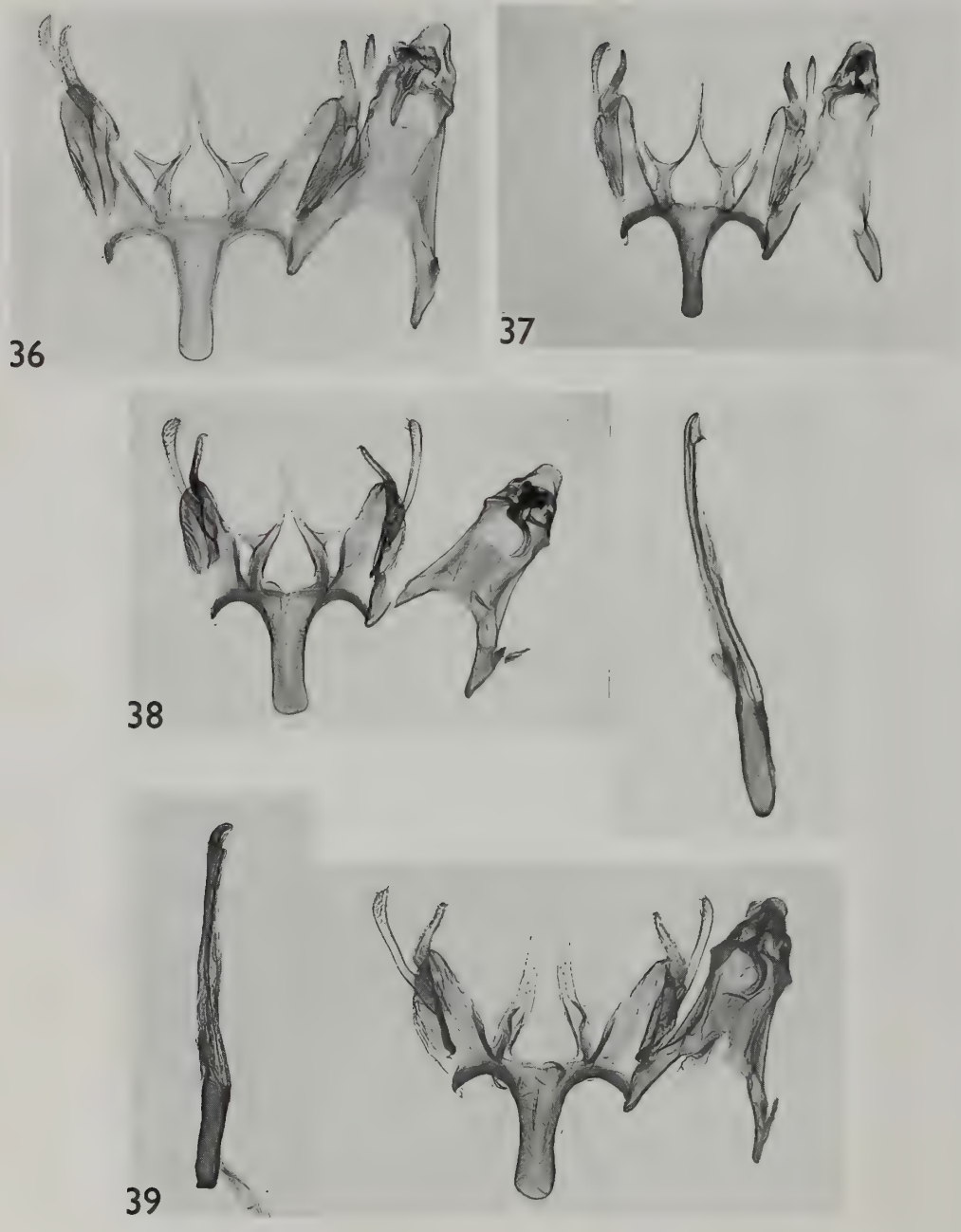


Figs 27, 28 Genitalia of *Sattleria* species. 27, male hybrid between *S. arcuata* and *S. pyrenaica*. 28, female *S. pyrenaica*.

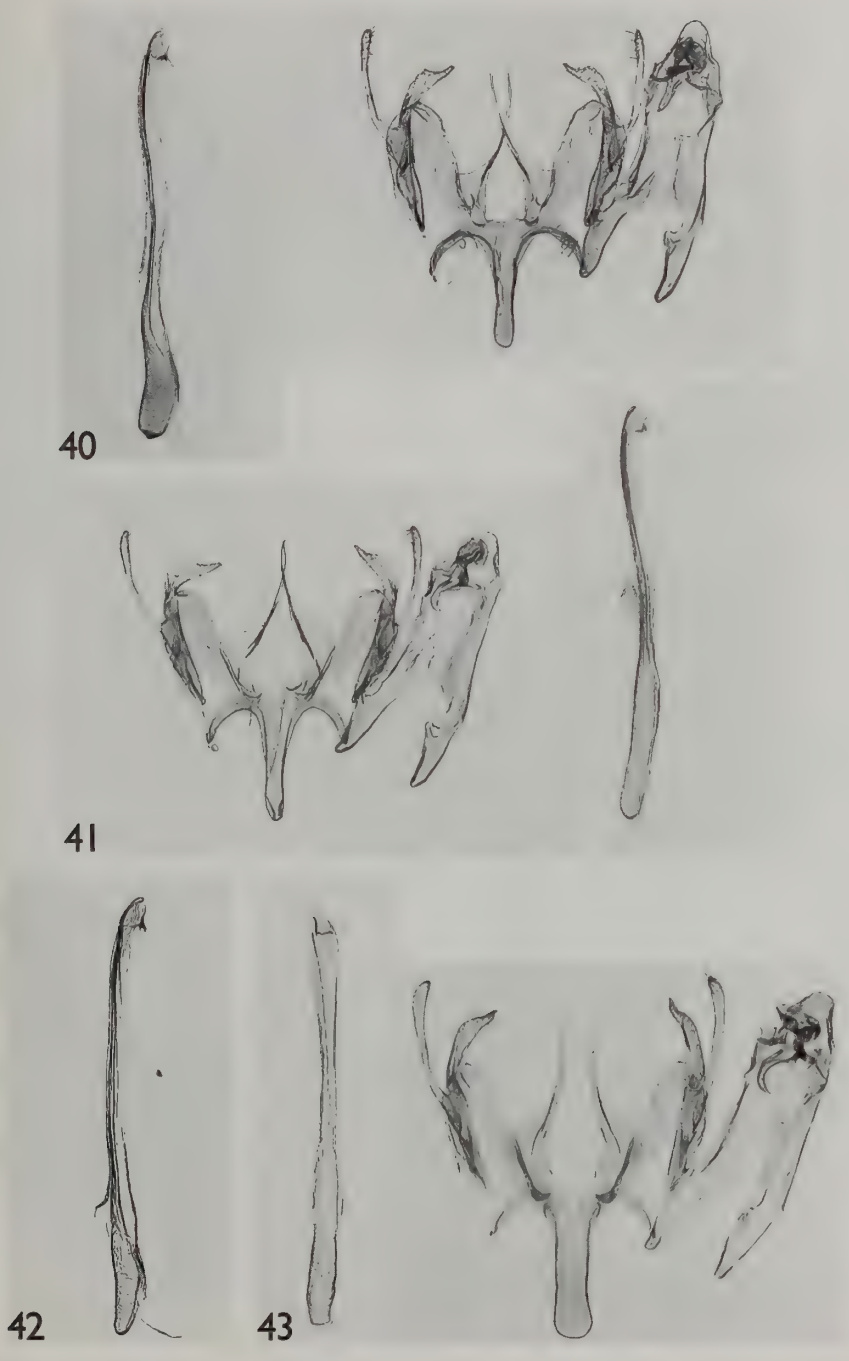


Figs 29–32 Male genitalia of *Sattleria* species. 29, *S. arcuata*. 30, *S. pyrenaica* (main form) and 31, variation in the aedeagus. 32, *S. pyrenaica* (eastern form).

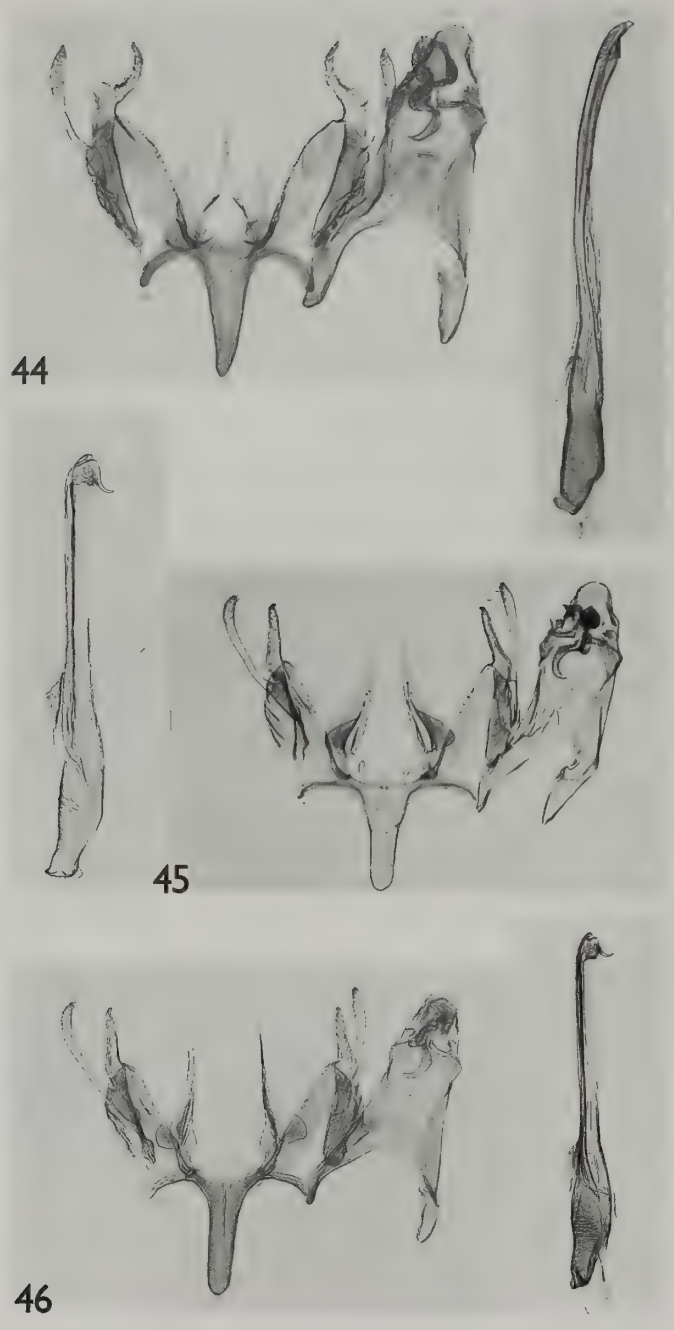
Figs 33–35 Male genitalia of *Sattleria* species. 33, *S. angustispina*. 34, *S. melaleucella* (form A, Switzerland: Glarner Alpen). 35, *S. melaleucella* (form B, N. Italy: 'Bozen').



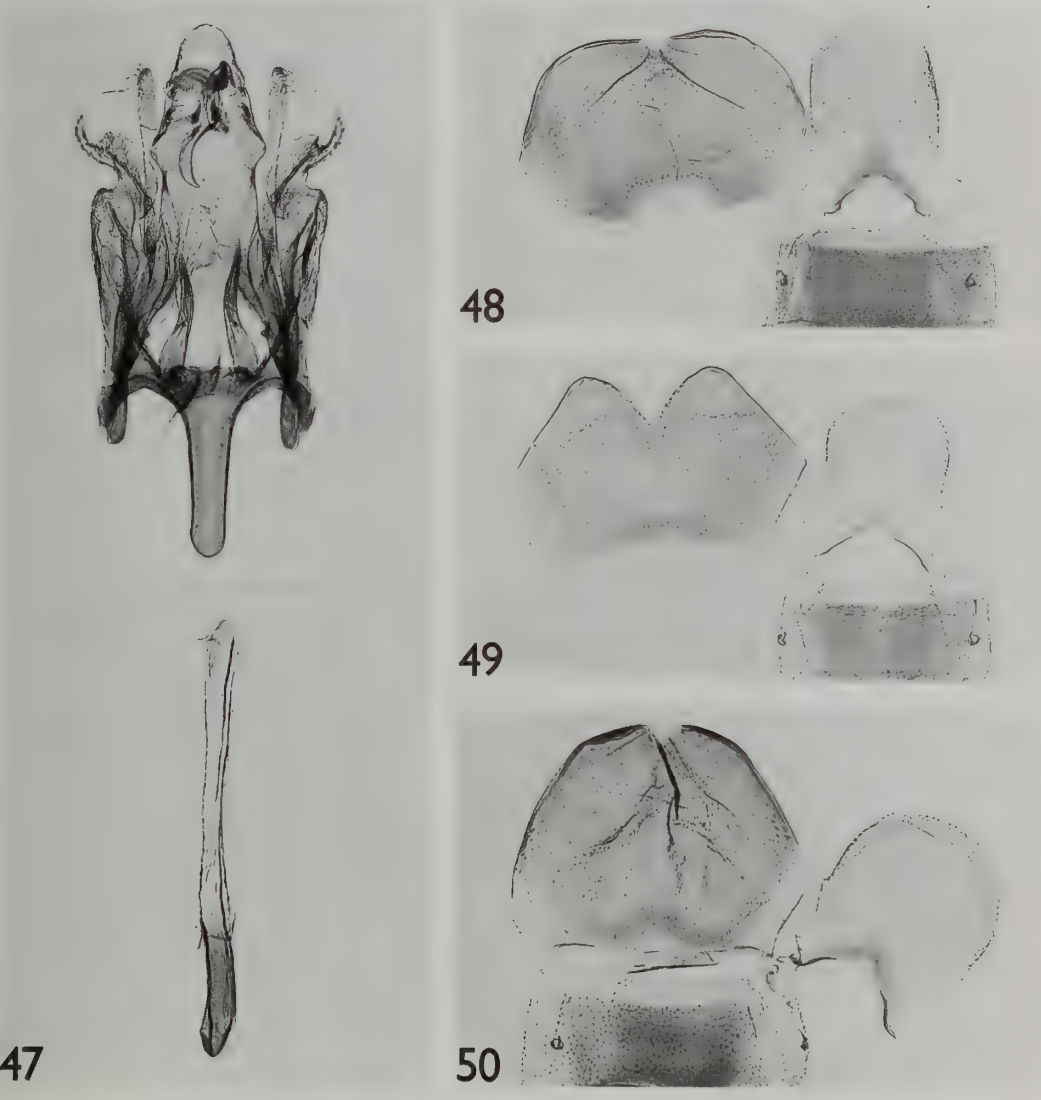
Figs 36–39 Male genitalia of *Sattleria melaleucella*. 36, form B, Italy: Appennino Abruzzese. 37, form B, France: Alpes Maritimes. 38, form C, Italy: Adamello. 39, form C, Italy: Adamello.



Figs 40–43 Male genitalia of *Sattleria* species. 40, *S. basistrigella basistrigella* (main form). 41, *S. b. basistrigella* (south-western form). 42, *S. b. triglavica* (aedeagus). 43, *S. b. triglavica*.

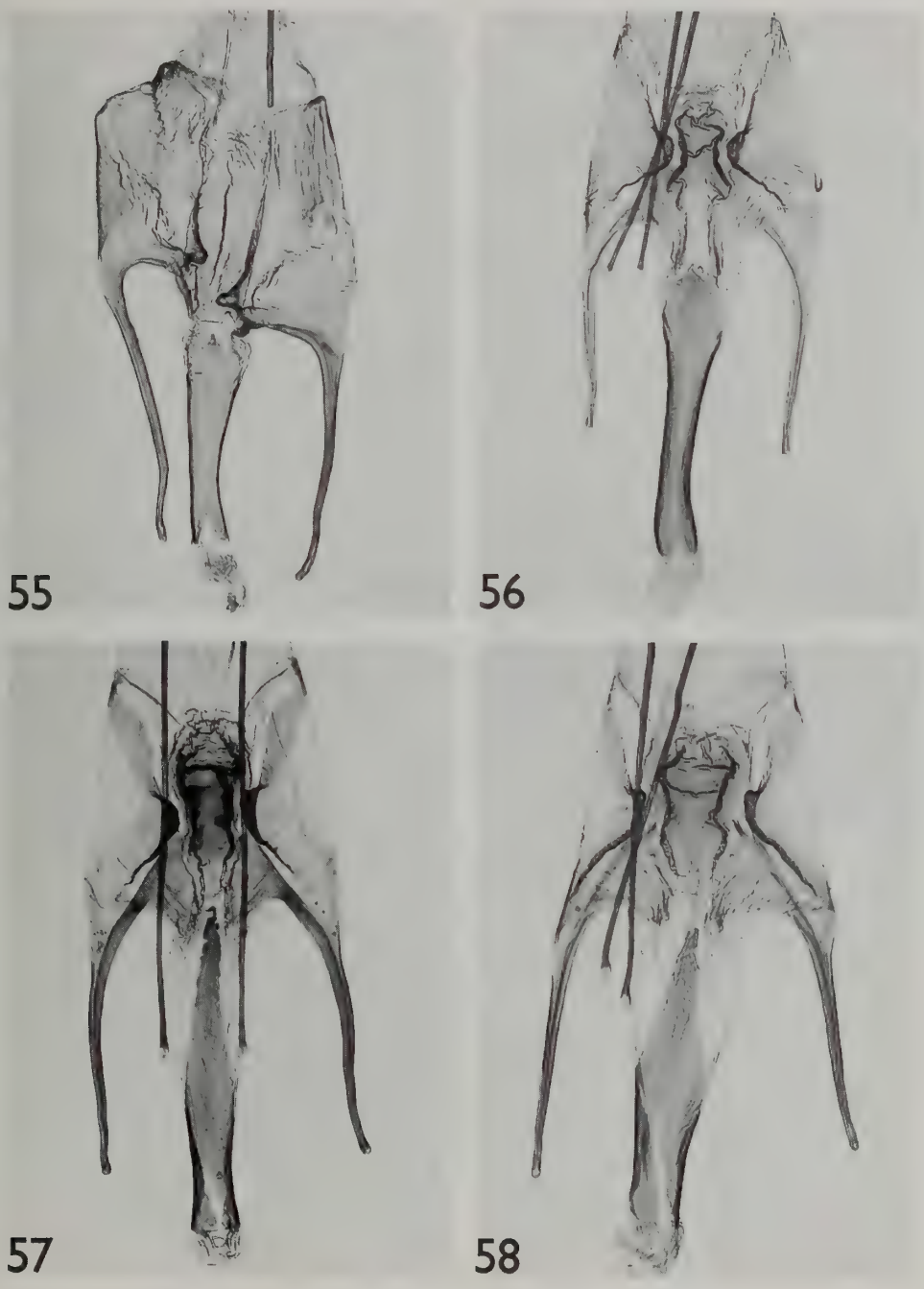


Figs 44–46 Male genitalia of *Sattleria* species. 44, *S. styriaca*. 45, *S. dzieduszyckii*, Tatry. 46, *S. dzieduszyckii*, southern Carpathians.



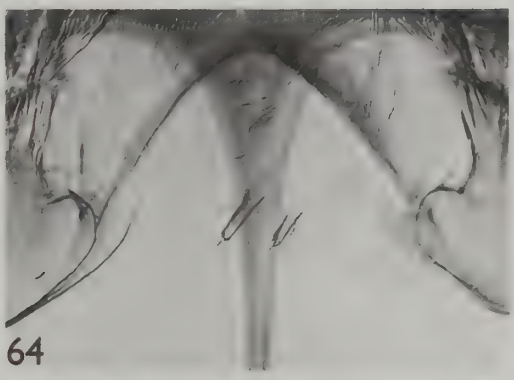
Figs 47–50 Male genitalia of *Sattleria* species. 47, *S. breviramus*. 48–50, eighth abdominal segments. (48) *S. arcuata*. (49) *S. pyrenaica*. (50) *S. angustispina*.

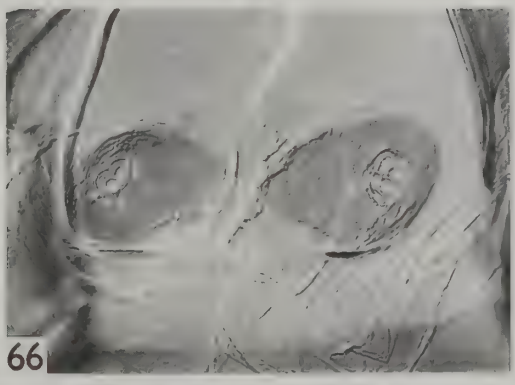
Figs 51–54 Female genitalia of *Sattleria* species. 51, *S. arcuata*. 52, *S. pyrenaica* (central Pyrenees). 53, *S. pyrenaica* (eastern Pyrenees). 54, *S. angustispina* (normal).



Figs 55–58 Female genitalia of *Sattleria* species. 55, *S. angustispina* (deformed). 56–58, *S. melaleucella*. (56) form B, Switzerland: Valais. (57) form A, Austria: Vorarlberg. (58) form A, Austria: Lechtaler Alpen.

Figs 59–62 Female genitalia of *Sattleria* species. 59, *S. basistrigella basistrigella* (main form). 60, *S. basistrigella basistrigella* (south-western form). 61, *S. styriaca*. 62, *S. dzieduszyckii*.





Figs 63–67 63, trace of signum in *Sattleria pyrenaica*. 64–66, male genitalia showing structures of the anellus region. (64) *Caryocolum marmoreum*. (65) *Agonochaetia terrestrella*. (66) *Sattleria melaleucella*. 67, larva of *Sattleria basistrigella*.

MATERIAL EXAMINED (including 10 ♂, 3 ♀ genitalia preparations)

Czechoslovakia/Poland: 1 ♂, 1868 (NM); 3 ♂, 1 ♀, Tatry, 1865, 1868, 1871 (NM); 1 ♂, 1 ♀, Tatry, 'Liljowe', 1950 m, 5.vii.1951 (BURM); 1 ♂, Tatry, 'Zawrat', 2000 m, vii.1950. **Rumania**: 15 ♂, 1 ♀, S. Carpathians, Bucegi Mts, Babele, 2200 m, 30.vii-2.viii.1984; 1 ♀, Bucegi Mts ('Bucsecs'), 4.viii.1907 (NM); 1 ♂, [Bucegi Mts,] Omul, 2400, 25.vii (MINGA); 1 ♂, [Bucegi Mts,] Mt Caraiman, 2200 m, 29.vi.1946 (MINGA); 3 ♂, [S. Carpathians, Fagarasului Mts,] Transylvania, Zurul ('Szurul'), 19.vii.1865 (ZI).

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INDEX

Principal references are in **bold**; invalid names are in *italics*.

Agonochaetia 210
Anacampsis 209
angustispina 207, 212, 214, 215, **217**, 218, 219
arcuata, 207, 212, 214, **215**, 216, 217, 219
Aristoteliinae 209

basistrigella 214, 215, 219, **221**, 222–224
breviramus 214, 215, **218**

Caryocolum 210, 212
Cosmardia 210

Dichomerinae 209
Doryphora 209
dzieduszyckii 206, 207, 209, 210, 212, 214–222, **223**, 224

figulella, Bryotropha 210
fusca 214, 218–221

Gelechia 209
Gelechiidae 205, 209, 210
Gelechiinae 205, 206, 209
Gelechiini 209
Gnorimoschema 209
Gnorimoschemini 205, 206, 209, 210

Klimeschiopsis 210

Lutilabria 210

maculosella, Acompsia 209
mariae 218, 219
melaleucella 212, 214–216, **218**, 219–221, 224
Mirificarma 207
Monochroa 209
myricariella, Teleiodes 210

petasitis, Scrobipalpopsis 209
Pogochaetia 210
pyrenaica 206, 207, 212, 214, 215, **216**, 217, 218, 224

salinella, Scrobipalpa 210
Sattleria 205–209, **210**, 212, 214, 215
Scrobipalpa 209
Scrobipalpopsis 209
styriaca 214, 215, 221, 222, **223**

tachyptilella, Bryotropha 210
tatrica 214, 224
Teleiodini 209
Teleiopsis 209
Tila 210
triglavica 214, 215, 221, **222**, 223

wilkella, Eulamprotes 210

Xystophora 209

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A review of wing reduction in Lepidoptera

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CONTENTS

Introduction 243
Terminology 245
Phases of wing reduction 245
Correlation between the reduction of wings and reduction in other organs 246
Teratological wing reduction 246
Feeding and flight 247
Courtship and flight 248
Oviposition and flight 248
Flight as an escape mechanism 248
Sedentary habit and locomotion in wing-reduced moths 249
Ovarial development and flightlessness 250
Wing reduction in males 251
Wing reduction in cold season moths 252
Wing reduction in oreal moths 254
Flight in a high temperature environment 255
Wing reduction in forest moths 256
Wing reduction in steppe and desert moths 256
Wing reduction in aquatic moths 256
Flightlessness in cavernicoles 256
Flightlessness in a butterfly inhabiting the communal nest of its larvae 257
Flight in Saturniidae 257
Check list of family-group taxa in which wing reduction occurs 258
Check list of the Microlepidoptera species, including Pyralidae, with wing reduction . 258
Discussion of wing reduction in different families 260
Acknowledgements 282
References 282
Index 285

SYNOPSIS. In Lepidoptera, wing reduction associated with loss of flight has evolved in many independent lineages in 25 of about 120 currently recognized families; however, less than one per cent of all known species are affected, reduction usually being confined to the female sex. The phenomenon of wing reduction is here examined throughout the Lepidoptera, the literature on the subject is reviewed, implications of flightlessness are discussed and the major hypotheses on the evolution of wing reduction are critically evaluated. A systematic list of family-group taxa in which wing reduction occurs is provided together with a list of all Microlepidoptera, including Pyralidae, known to be wing-reduced. An overview of the 25 families with wing-reduced taxa is given and a number of examples are illustrated.

INTRODUCTION

The acquisition of wings suitable for sustained directional flight undoubtedly played a crucial part in the evolution of insects and is a major reason for their success. The advantage of flight lies in greatly enhanced possibilities for the location of food sources for the adults and host-substrates for their early stages, mate location, dispersal and escape from predators. The possible

role of the wings in maintaining the thermal balance of an insect by providing a large surface area for the exchange of heat with the environment must also be considered. Yet in spite of such seemingly obvious benefits, a smaller or larger number of species within most major insect orders, for example Hemiptera, Coleoptera, Hymenoptera, Diptera, Neuroptera and Lepidoptera, have secondarily lost the ability to fly, sometimes in only one sex, whilst the wings have undergone various degrees of reduction culminating in their complete loss.

The Lepidoptera are characterised by two pairs of scale-covered wings, but within the order a considerable degree of wing shape diversity can be observed. The most primitive Lepidoptera have broadly lanceolate wings with a short fringe; fore and hind wings are of the same shape and size and have similar (homoneurous) venation. In higher, heteroneurous Lepidoptera the number of wing veins is somewhat reduced and, as the hind wing has lost more veins than the fore wing, both pairs are dissimilar. In many Microlepidoptera, for example Nepticulidae, Gracillariidae and Coleophoridae, the hind wing is very narrow, but this reduction is compensated by a greatly extended fringe. Similarly in Alucitidae and Pterophoridae both pairs of wings are divided into narrow branches which are connected and surrounded by long fringes. If the wings play a significant part in heat regulation such modifications of their shape may be a means of reducing the heat-exchanging wing surface without losing the aerodynamic benefits of the larger wing area. In numerous groups of Lepidoptera some genuine reduction of one pair of wings, usually the hind wings, can be observed, for example in the males of the Australian genera *Tympanota* Warren and *Sauris* Guenée (Geometridae) (Dugdale, 1980). Amongst the more extreme examples are the Indian himantopterine Zygaenidae with filiform hind wings and the male of the South American *Diptilon culex* Draudt (Arctiidae, Ctenuchinae) with hind wing vestiges so small that they are concealed in the metathoracic hair cover. However, as such specialisations, even when extreme, do not render the affected insects flightless, this phenomenon is not pursued further in this paper. By contrast, the presence of fully developed, seemingly functional wings is no indication that they are actually used, and there is ample evidence that some species are more active fliers than others. Females especially are frequently sluggish and those of many species rarely take to the air before they have mated and deposited at least part of their egg complement; but flightlessness without wing reduction is also outside the scope of this review.

In the Lepidoptera flightlessness coupled with some degree of wing reduction, usually brachyptery, is an exception and affects less than one per cent of the currently known 150,000–200,000 species. Nevertheless, wing-reduced species are recorded in 25 out of the 120 or so currently recognised families, representing 11 of the 38 superfamilies. In the primitive, non-ditrysian families wing reduction is unknown except in a few Hepialidae; it is also unknown in the ditrysian superfamilies Cossoidea, Castniodea, Sesioidea, Immoidea, Alucitoidea, Pterophoroidea, Calliduloidea, Hedyloidea, Hesperioidea, Papilionoidea, Mimallonoidea and Sphingoidea.

Although wing reduction in Lepidoptera is not a uniform phenomenon, and each case should be looked at on its own merit, a number of general principles are recognizable. It has evolved many times independently and is a positive strategy, not an evolutionary blind alley that leads to early extinction. There is no apparent phylogenetic predisposition to such reduction; it can evolve in any family, provided specific preconditions are met. Wing reduction is almost exclusive to the female sex, but in rare instances has evolved in both sexes. Reduced wings are frequently correlated with reduced mouthparts and, where applicable, reduced tympanal organs; in females there is also a correlation with an extension of the ovaries into the thorax. In most instances reduction has occurred either as a consequence of sedentary habit or in response to certain environmental factors. Species of the first category have more or less reduced legs whilst those of the second category have retained full use of their legs and are able to run and sometimes jump. Wing reduction in response to environmental conditions occurs mainly in species that are endemic to small oceanic islands, or inhabit the alpine zone of high mountains, or have their adult activity period in the cold season.

According to Dierl & Reichholf (1977: 30) wing reduction mainly occurs within small systematic units such as genera or groups of genera in which it affects all or most species. Examples in support of this contention are *Diurnea* Haworth and *Cheimophila* Hübner (Oecophoridae), *Ceuthomadarus* Mann (Lecithoceridae) and many genera of Geometridae. However, an analysis on a world basis indicates that wing-reduced species are more frequently the exception within large genera of fully winged species, for example *Pharmacis* Hübner (Hepialidae); *Tinea* Linnaeus, *Eudarcia* Clemens (Tineidae); *Kessleria* Nowicki (Yponomeutidae); *Ethmia* Hübner, *Thyrocopa* Walsingham, *Borkhausenia* Hübner, *Pleurota* Hübner (Oecophoridae); *Elachista* Treitschke (Elachistidae);

Symmoca Hübner (Symmocidae); *Kiwaia* Philpott, *Ephysteris* Meyrick, *Caryocolum* Gregor & Povolný, *Stomopteryx* Heinemann (Gelechiidae); *Oxypteron* Staudinger (Tortricidae); *Synaphe* Hübner, *Catoptria* Hübner, *Orocrambus* Purdie (Pyralidae); *Xanthorhoe* Hübner, *Elophos* Boisduval (Geometridae); *Orgyia* Ochsenheimer (Lymantriidae); *Xestia* Hübner, *Agrotis* Ochsenheimer (Noctuidae) and others. It should therefore not be assumed automatically that wing reduction affects all members of a genus if it is known to occur in one of them. For example, Dierl (1983: 141) implies that the females of all species of *Estimata* Kozhanchikov (Noctuidae) are brachypterous, although those of all but one species are still unknown.

In almost all cases wing reduction is restricted to the female sex whilst the male retains fully developed wings and the ability to fly. Wing reduction in both sexes is extremely rare; it is recorded in 10 different families and affects only about 25 species, most of them inhabitants of southern ocean islands. Flightlessness with wing reduction affecting solely the male sex is so far unknown in Lepidoptera.

Terminology

Depending on the state of their wings and the degree of reduction, Lepidoptera can be classified as macropterous, brachypterous, stenopterous, micropterous or apterous; however, these are not clear-cut categories and the terminology is often applied loosely, in particular the term brachyptery, which may encompass stenoptery and microptery. The classification is restricted to the wing itself and disregards the associated flight musculature and the actual ability to fly. See also Hackman (1966: 2).

Macropterous — species with fully developed wings (e.g. Figs 1, 3, 5, 9). Macropterous species are usually but not always capable of flight. For example the macropterous female of *Lymantria dispar* (L.) (Lymantriidae) is more or less flightless.

Brachypterous — species showing various degrees of wing reduction (e.g. Figs 2, 4, 6–8, 12). In a living brachypterous moth the wings are usually exceeded to a greater or lesser extent by the abdomen. The wing shape is broadly lanceolate and one or more veins are lost, although some tubular veins are retained, at least in the fore wing. The hind wing may be further reduced than the fore wing and may have lost all tubular veins (for example in *Sattleria* ♀), but often retains the frenulum. Brachypterous moths are incapable of sustained flight.

Stenopterous — species with the fore wing strongly reduced in width but without any significant reduction in length. The hind wing is also reduced and may be vestigial although the frenulum is usually present. Stenoptery is very rare but is observed, for example, in the females of *Pleurota marginella* (Denis & Schiffermüller) (Oecophoridae) (Fig. 10; Spuler, 1910: 341, pl. 88, fig. 69b, as *P. rostrella* Hübner) and *Spartopteryx kindermannaria* (Staudinger) (Geometridae) (Fig. 45; Wehrli, 1941: 466, pl. 41b). Stenopterous moths are incapable of flight.

Micropterous — species with both pairs of wings reduced to small unstructured lobes (Figs 32, 60). All tubular veins are lost and the upper and lower wing membranes are often separated. The hind wing vestige has also lost the frenulum, for example, *Erannis defoliaria* (L.) (Geometridae); *Chondrostega* species (Lasiocampidae).

Apterous — species without any external remnants of wings. Aptery is very rare and, where it occurs, is confined to the females; no species with apterous males is known. Certain species sometimes referred to in the literature as 'apterous' or 'wingless' still have external wing vestiges, for example some geometrid winter moths. An example of true aptery is the female of *Cheimoptena pennigera* Danilevsky (Danilevsky, 1969*a*: 182, fig. 10).

Phases of wing reduction

In various Lepidoptera sexually dimorphic wing shapes can be observed. Such dimorphism may reflect the different flight requirements of the sexes resulting, for example, from their different body weight; however, even if small, it may be the first indication of a trend towards wing reduction in the female.

The reduction of the wings follows a distinct evolutionary (but not phylogenetic) sequence and examples of all intermediate stages between macroptery and aptery are found. Initially the distal half of the fore wing becomes narrower; if a distinct tornus was present this is reduced until the wing margin (dorsum and termen) is an even curve from base to apex and the formerly triangular wing has become broadly lanceolate. Simultaneously the hind wing changes shape and in broad-winged forms also becomes lanceolate.

The slight sexual wing dimorphism in *Chionodes pergrandella* (Rebel) (Gelechiidae) (Burmann, 1977: figs B2 ♂, B3 ♀, as *C. decolorella)* from the European Alps and Central Asia is seen as an example of an early stage in the development of female brachyptery (Sattler, 1986: 258–259). In

the male the costal and dorsal margins of the fore wing diverge towards the termen, and the wing is distinctly wider at two-thirds than at one-third whereas in the female both margins run almost parallel and the wing is not wider at 2/3. The hind wing termen of the female is more oblique than that of the male and the apex is more pointed.

In *Thyrocopa apatela* (Walsingham) (Oecophoridae, Xyloryctinae) (Figs 7, 8; Zimmerman, 1978: figs 645, 650, ♀) from Hawaii wing reduction is further advanced. Both wings have become lanceolate and the venation in the distal half is much condensed. In the fore wing R4 and R5 are almost coincident and one M vein is lost; in the hind wing M3 and CuA1, which are usually connate in *Thyrocopa* Meyrick, have migrated onto a common stalk. The hind wing is significantly smaller than the fore wing, whereas in other members of this genus they are of about equal size.

Further simplification of the venation is followed by withdrawal of the veins from the wing margin (accompanied by loss of the marginal sensilla campaniformia) and gradual loss of the tubular structure of the remaining veins (Baus, 1936: 45). For example, in the fore wing of *Areniscythris brachypteris* Powell (Scythrididae) from California only part of Sc, the R stem with traces of R5 and sometimes R4, and the partly obsolete M3 and 2A are present whilst the hind wing venation is reduced to just traces of Rs and 2A (Powell, 1976*b*: figs 2, 3, ♀).

With the loss of the tubular veins the upper and lower membranes of the wing vestiges become separated and the sensilla campaniformia are lost except for some of those on the wing base (Baus, 1936: 45). This stage is reached in the vestigial wings of *Erannis defoliaria* (L.) (Geometridae) female. Complete loss of the wings is known in the females of certain Psychidae (Dierl, 1973) and Heterogynidae (Daniel & Dierl, 1966, figs 2, 3) but is also recorded, for example in *Cheimoptena pennigera* Danilevsky (Geometridae) (Danilevsky, 1969*a*: 183, fig. 10), *Orgyia ericae* (Germar) and *O. dubia* (Tauscher) (Lymantriidae) (Heitmann, 1934: 180). No cases of aptery in male Lepidoptera are known.

The frenulum is lost at a very late stage in the reduction process. It is still present on the rudimentary hind wings of *Pleurota marginella* (Denis & Schiffermüller) (= *rostrella* Hübner) (Oecophoridae) and *Sattleria* Povolný (Gelechiidae), which have lost all tubular veins, but is absent from the hind wing vestiges of *Erannis defoliaria* (L.) and others.

The reduction of the hind wing and its venation progresses faster than that of the fore wing. For example the stenopterous female of *Pleurota marginella* (Denis & Schiffermüller) and brachypterous females of *Sattleria* spp. retain still most of their original venation in the fore wings whilst the vestigial hind wings have lost all tubular veins.

Correlation between the reduction of wings and reduction in other organs

The correlation between wing reduction and reduction of the mouthparts was investigated and discussed in detail by Naumann (1937). A tendency towards reduction of the mouthparts is widespread in the Lepidoptera, and examples of a reduced proboscis are found in most families, although there are fewer in groups of strong fliers such as the Sphingidae and Noctuidae and, as to be expected, very few in the butterflies, for example some African Lycaenidae of the subfamily Lipteninae (Eliot, 1973: 394). In fully winged species the mouthparts are mostly developed equally in both sexes whereas in those with wing reduction in the female the male has a longer proboscis. Nevertheless, in such species the male proboscis (in relation to the body length) is shorter than in related fully winged species, which indicates that mouthpart reduction affects both sexes, even though it is distinctly more advanced in the female. Differences in the length of the proboscis between macropterous males and wing-reduced females raise the question whether in some instances the former may still feed whilst the latter no longer do so.

A close correlation between wing reduction and the reduction of the tympanal organs in Geometridae, Lymantriidae, Arctiidae and Noctuidae was observed and discussed in detail by Heitmann (1934) and Gohrbandt (1938) (see also p. 250).

Teratological wing reduction

In most macropterous Lepidoptera individuals with imperfectly developed wings are occasionally observed. Failure to expand the wings properly, following emergence from the pupa, is usually the result of mechanical damage or other unfavourable influences, such as lack of moisture during the pupal or perhaps larval stage. According to some observers the females are more susceptible to such damage than the males. Crippled individuals frequently result from pupae that were kept too dry, and even the condition of the host-plant during the larval stage may be significant. For example, Loritz (1952) considered casual brachyptery in females of *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Thaumetopoeidae) reared in captivity to be the result of desiccated larval food.

Apart from the failure to expand an otherwise normally developed wing completely, the loss of one or more wings, usually a hind wing, is also known and is commonest in the Geometridae. During a mass occurrence of *Eulype hastata* (L.) (Geometridae) in Finland in 1947 Hackman (1966: 2) observed that for an unknown reason about 25% of all specimens lacked one or both of their hind wings. Burmann linked a similar observation on *Semiothisa clathrata* (L.) (Geometridae) in Austria to the influence of an unidentified herbicide on the host-plants of the larvae. Many of the *clathrata* examined in a locality near Innsbruck lacked one or rarely both of their hind wings (Burmann, 1973: figs 1–5); two individuals of *Perizoma blandiata* (Denis & Schiffermüller) (Geometridae) with the same defect were also observed. Amongst the defective individuals both sexes were represented in about equal numbers and the affected wings were lost completely, without any trace of external rudiments. The F1 generation reared from one normal and two defective *clathrata* females had normal wings.

Knatz (1891) assumed accidental deformation of the wings, resulting from unfavourable influences during the larval or pupal period, to be the primary cause of wing reduction. Males thus affected would simply perish without a chance of finding a mate, whereas females rendered flightless would still be fertilized. Continued over long periods this effect would be increased and finally lead to wing reduction in the female. As a result the thorax would become smaller and the abdomen larger with the ovaries increasing in size. The mouthparts of the males of such species would be reduced because the male would have to spend more time in search of the non-motile female and consequently would have less time for feeding. Moreover, its chances of meeting the (non-motile) female at the food source would be diminished. However, it is unlikely that accidental wing deformation has played a significant role, if any at all, in the evolution of flightlessness and wing reduction because no selective advantage to the female can be demonstrated.

Feeding and flight

For reasons of longevity, slow progressive maturing of the ova after emergence of the female from the pupa, energy-intensive courtship, search and dispersal flights, migration etc., many adult Lepidoptera must feed to supplement the energy that was stored at the larval stage. They take energy in the form of pollen, nectar, decaying fruit and other plant material, sap from injured trees and other usually liquid substances, and flight plays so important a part in the search for such non-ubiquitous food sources that non-feeding must be considered one of the preconditions for the evolution of flightlessness. It is therefore not surprising to find that certain species with wing reduction were pre-adapted in that respect, because they are members of generally non-feeding families in which mouthpart reduction is a family characteristic, for example Hepialidae, Psychidae, Lasiocampidae and Lymantriidae. However, other wing-reduced species, although themselves having reduced mouthparts, are more or less closely related to taxa which have fully developed apparently functional mouthparts. For example, in *Apocheima* Hübner and *Lycia* Hübner, both genera with wing-reduced females, the mouthparts are reduced, whereas in the closely related but fully macropterous genus *Biston* Leach (Geometridae) they are well developed.

Similarly, in *Ethmia charybdis* Powell (Oecophoridae, Ethmiinae), a species with brachypterous females, the mouthparts are reduced (Powell, 1971: 31) whereas in other species of *Ethmia* Hübner they are well developed. For example, in *E. aurifluella* (Hübner) and *E. lineatonotella* (Moore), both sexes fully winged, the distal portion of the proboscis bears characteristic sensilla styloconica (Sattler, 1967: pls 12, 13), which are chemoreceptors, possibly sensitive to sucrose (Städler *et al.*, 1974: 63). Their presence suggests that such species may feed; however, within *Ethmia* various degress of reduction of the proboscis and the labial and maxillary palpi are known (Sattler, 1967: 10, pl. 11) and indicate that there may be a general shift away from feeding. It is possible that even a somewhat reduced proboscis is still used to take in water, which is readily available as rain or condensation in most habitats, to counteract desiccation. Non-feeding may have been an important pre-adaptation in certain moths that facilitated a shift of their adult activity period to the cold season with its absence of flowers and paucity of other energy sources.

According to Tweedie (1976) abstention from feeding as an adult is the main cause of wing reduction in the female. A non-feeding female will have a heavy abdomen as a consequence of having to store enough nutrient in the larval stage for its full egg complement. This causes reduction of flight activity and eventually results in reduction of unused flight organs. However, whilst non-feeding is a precondition to flightlessness, it is unlikely to be the main factor in its evolution, because there are successful strategies available to maintain the ability to fly when the body weight is increased.

Courtship and flight

The importance of flight in the courtship process of the Lepidoptera and the crucial role of the male in mate locating must be seen as the major reason why flightlessness and wing reduction are usually restricted to the female and are only found exceptionally in the male (see p. 251). In most Lepidoptera the male alone is responsible for finding a mate. It is usually guided to its target by pheromones emitted by a stationary female, and tacking against the wind, often flying close to the ground, is the most effective means of scanning a large area for a pheromone plume. Even in those groups in which the female is attracted to the male at some stage in the courtship process, flight remains essential for the latter to fulfil its role, for example by congregating with other males on flowers, where the sexes meet (Micropterigidae), performing courtship dances (Hepialidae), forming courtship swarms (Adelidae) or setting up and defending territories (butterflies) to which the females are attracted. Intrasexual competition in that process acts as a powerful effective barrier against flightlessness in the male, whereas in most Lepidoptera no such constraints act upon the female. Similarly, a mate locating system that requires active participation of the female is an obstacle to the evolution of flightlessness in that sex.

Oviposition and flight

Most Lepidoptera live in a non-homogeneous environment where flight is essential or at least highly advantageous to the female in locating a suitable oviposition site. The larvae of many species, in particular those of most Microlepidoptera, are highly host-specific. They often feed on annual plants and other non-permanent, discontinuous food sources, and their respective host-plants are not always available in the immediate vicinity of a freshly emerged female. For example, annual plants die off during the winter, and fresh plants may have appeared elsewhere when the female emerges from an overwintered pupa. Some larvae also undergo a change of diet, as a consequence of which pupation may take place at some distance from their initial host-plant. For example, the first instar larvae of Adelidae mine the leaves of certain living plants whilst later instars are scavengers amongst leaf litter on the ground. In all such instances the female has to find the host-plant of the first instar larva for oviposition, and the selective advantage of flight in this process is so great that flightlessness would only have a chance to evolve in a habitat that is sufficiently permanent and continuous to allow non-selective oviposition. Such a condition is met in species with larvae that are omnivorous (*Pringleophaga* Enderlein, Tineidae), scavengers (various Tineidae, Psychidae, Oecophoridae, Lecithoceridae, Symmocidae), polyphagous (most cold season Oecophoridae and Geometridae; Lymantriidae) or host-specific but inhabiting single species plant communities or sites in which their host-plant dominates.

A number of species with brachypterous females or with wing reduction in both sexes inhabit grassland, which constitutes a permanent, continuous habitat. Their larvae feed on roots or green tissue, often apparently without specialization on a particular grass species. Grassland inhabitants are *Pharmacis* spp. (Hepialidae), *Embryonopsis halticella* Eaton (Yponomeutidae), *Pleurota marginella* (Denis & Schiffermüller) (Oecophoridae), *Elachista* spp. (Elachistidae), *Megacraspedus* spp. and probably *Ephysteris* spp. (Gelechiidae), *Catoptria* spp. and *Exsilirarcha graminea* Salmon & Bradley (Pyralidae, Crambinae, Scopariinae) and others. A few cold season species are apparently monophagous on certain trees, e.g. *Exapate duratella* (Heyden) (Tortricidae) on *Larix* and the Geometridae *Erannis ankeraria* (Staudinger) on *Quercus* and *Alsophila quadripunctaria* (Esper) on *Acer*, and it is likely that a single tree of adequate size can act as an island large enough to sustain a viable population over many years.

Flight as an escape mechanism

Many Lepidoptera react to disturbance of their immediate vicinity, for example vibrations caused by an approaching person or animal, by flying away. The question has to be asked whether flight is essential in avoiding danger or whether a species could adequately protect itself by other means were it to lose the ability to fly. The greatest danger to adult Lepidoptera is predation, primarily by vertebrates (insectivorous birds, mammals and reptiles), but whilst flying undoubtedly provides an important escape mechanism, there are also numerous other successful strategies. These include living under conditions of naturally reduced predator pressure as they prevail, for example, on low diversity oceanic islands (Gressitt, 1970: 316), possibly on high mountains, or during the cold season of the northern hemisphere (Dierl & Reichholf, 1977: 33). When at rest individuals can hide in inaccessible places such as scree, dense vegetation, under bark etc., or rely on cryptic coloration. Many species are protected by unpalatable or poisonous hairs or

substances and advertise this fact by aposematic coloration. The loss of flight still leaves other forms of motility such as running, jumping or simply dropping to the ground, often followed by feigning death. All these strategies, individually or in combination, are widely and successfully employed in Lepidoptera and indicate that the need to avoid predators would be no insurmountable obstacle to flightlessness. There is even evidence that the wing-reduced sex sometimes may be better protected from predators than the fully winged one. For example, in the Alps, Pinker (1953: 179) and Burmann (1956) observed very heavy bird predation on the macropterous males of *Lycia alpina* (Sulzer) (Geometridae) whilst the equally common brachypterous females were apparently ignored by the predators.

Sedentary habit and locomotion in wing-reduced moths

Without the need to fly for purposes of feeding, mating or ovipositing the females of certain species, for example Psychidae, Heterogynidae, Lymantriidae and Artiidae, have become more or less sedentary, in extreme cases even followed by a partial reduction of their legs. The sedentary females remain near, on or inside the pupal cocoon; those of certain Psychidae do not even emerge from the pupa, for example *Thyridopteryx ephemeraeformis* (Haworth) (Davis, 1964: 11, figs 144, 145) or *Megalophanes viciella* (Denis & Schiffermüller) and others (Dierl, 1973: 3). Mating takes place in situ and the eggs are deposited in one batch on the pupal cocoon (*Orgyia* Ochsenheimer, Lymantriidae), in the larval/pupal case (many Psychidae) or in the pupal exuviae (some Psychidae; Heterogynidae). By contrast, the brachypterous females of most other species have retained some degree of motility and normally are capable of running and climbing. The larvae of many cold season moths, such as *Diurnea* Haworth (Oecophoridae), *Exapate congelatella* (Clerck) (Tortricidae) and many Geometridae, are polyphagous on deciduous trees and pupate on the ground. After emerging from the pupae such females are able to find and ascend a tree, where mating and ovipositing take place. In sparsely vegetated alpine habitats with limited stands of the host-plant, flightless females of the motile type are able to move between plants and disperse their egg complement. For example, in the almost barren habitat of *Sattleria melaleucella* (Constant) in the Lechtaler Alpen the main host-plant in that locality, *Saxifraga biflora* subsp. *macropetala*, grows in clusters which are often too small to accommodate all the offspring of one female so that some motility is advantageous.

Several observers have specifically commented on the remarkable ability of certain brachypterous moths for making short jumps, covering distances of about 5 cm or more; however, jumping is sometimes also observed in species that normally fly. Petry (1904: 6) described the movements of the males of *Acompsia dimorpha* Petry (Gelechiidae), which approached a freshly emerged female in early morning, as more hopping than flying ('mehr hüpfend als fliegend'). Jumping as an escape mechanism was observed in *Scythris inspersella* (Hübner) (Scythrididae), a fully winged species that normally flies; the adults visit various flowers from which they jump to the ground rather than fly away when disturbed (Sattler, 1981: 16). As a regular behaviour jumping is known in both sexes of the fully winged but nevertheless flightless Gelechiidae *Gnorimoschema bodillum* Karsholt & Nielsen from Denmark (Karsholt & Nielsen, 1974: 96) and *Scrobipalpula* sp. from the Falkland Islands (Kirke, pers. comm.); exceptionally it also occurs in the male of *Sattleria melaleucella* (Constant) (pers. obs.), which is capable of normal flight. Jumping as a regular means of locomotion or in response to disturbance has been recorded in the brachypterous females of *Kessleria zimmermanni* Nowicki (Yponomeutidae); *Thyrocopa apatela* (Walsingham) (both sexes), *Atomotricha ommatias* Meyrick, *Pleurota marginella* (Denis & Schiffermüller) (Oecophoridae); *Elachista galatheae* (Viette) (Elachistidae) (both sexes); *Kiwaia jeanae* Philpott (both sexes), *Caryocolum laceratella* (Zeller), *Sattleria* species (Gelechiidae); *Areniscythris brachypteris* Powell (Scythrididae) (both sexes); *Sorensenata agilitata* Salmon & Bradley (probably both sexes, female unknown), *Sphaleroptera alpicolana* (Frölich) (Tortricidae); *Campbellana attenuata* Salmon & Bradley (Carposinidae) (both sexes) and *Exsilirarcha graminea* Salmon & Bradley (Pyralidae) (both sexes). The presence of this habit in at least eight different families, representing the superfamilies Yponomeutoidea, Gelechioidea, Tortricoidea, Copromorphoidea and Pyraloidea, is an indication that it may have evolved many times independently from the moths' normal take-off mechanism for flying.

Although widespread in wing-reduced Lepidoptera, jumping appears to be restricted to species that live on the ground in places with exposed soil and sparse vegetation, for example *Thyrocopa apatela* (Walsingham), *Sattleria* species, *Areniscythris brachypteris* Powell, or in dense grass, for example *Elachista galatheae* (Viette), *Pleurota marginella* (Denis & Schiffermüller), *Exsilirarcha*

graminea Salmon & Bradley, sometimes *Sattleria* species. This habit is not developed in motile tree-living moths such as *Diurnea* species and the various geometrid winter moths (*Alsophila* Hübner, *Operophtera* Hübner, *Erannis* Hübner and others), nor in the Psychidae and the females of heavy-bodied moths (Lasiocampidae, Lymantriidae, Arctiidae), many of which are sedentary. According to Harper (1990: 44) the brachypterous female of *Diurnea fagella* (Denis & Schiffermüller), when disturbed while at rest on a tree trunk, drops slowly, its fall apparently controlled by the outstretched wings. Although the descent is not vertical but proceeds at an angle it cannot be described as true gliding. Little is known about locomotion in the wing-reduced Noctuidae on southern ocean islands, but it would not be surprising if at least the micropterous *Dimorphinoctua cunhaensis* Viette were capable of jumping.

Whilst in the wing-reduced females of certain Psychidae, Heterogynidae, Lasiocampidae, Lymantriidae and Arctiidae the legs are more or less strongly reduced as a consequence of their sedentary habit, there is little evidence that in wing-reduced but motile species the legs are better adapted to running or jumping than in their fully winged close relatives that fly. According to Powell (1976*b*: 328) *Areniscythris brachypteris* Powell (brachypterous in both sexes) possesses longer tarsi and a 1.5 times thicker hind femur than several other Scythrididae of comparable size; however, those differences are relatively slight. Moreover, the systematic position of *Areniscythris* Powell is still somewhat unclear and it is therefore uncertain whether the examined *Scythris* species are systematically close enough for a meaningful comparison. The legs of *Thyrocopa apatela* (Walsingham) (brachypterous in both sexes) do not differ noticeably from those of fully winged *Thyrocopa* species and there are no appreciable differences in leg structure between the macropterous flying males and brachypterous running and jumping females of *Sattleria* species. No comparative studies of the leg musculature in jumping and non-jumping moths are available, but if we consider jumping as merely a behavioural remnant of the normal take-off for flight, the absence of special adaptions for that means of locomotion would not be surprising.

Ovarial development and flightlessness

In broad agreement with several previous authors (Naumann, 1937; Eggers, 1939; Downes, 1964; Hackman, 1966) the crucial initial factor in the process that leads to flightlessness and wing reduction in the females is seen in the degree of maturity the eggs have reached when the adult emerges from the pupa. Those species in which they mature gradually after the female has left the pupa must be relatively long-lived and depend on feeding to sustain themselves and obtain extra energy for the development of the eggs. The importance of flight in the search for food sources makes it unlikely that flightlessness evolves in such moths or, for the same reason, in many butterflies. By contrast, females that emerge from the pupa with a fully mature egg complement are able to mate and oviposit immediately, before the first flight, if other conditions permit. For example, if the male is attracted to the female and the larvae are generalist rather than specialist feeders, oviposition can take place more or less on the spot without the female having to search for a mate or a specific host-plant and therefore without gaining any significant advantage from the ability to fly. Such species can afford to be short-lived and thus need not feed. A short adult life span would also reduce the exposure of the egg-laden female to predators.

An increase in the number of fully developed eggs is accompanied by an increase in ovarial size, and the growing ovaries gradually displace the tracheal air sacs and tympanal organs, where present, resulting in a heavier abdomen. The main function of the tympanal organs being the detection of ultrasonic cries of insectivorous bats (Spangler, 1988), the loss of that organ is of little consequence to non-flying moths, whilst conversely it is advantageous to a moth that has lost its hearing ability to avoid flying and thus not expose itself to such predators. With a further increase in size the ovaries of various species extend more or less deeply into the thorax, for example in *Orgyia* Ochsenheimer (Lymantriidae) (Heitmann, 1934: 174–180) and *Ocnogyna* Lederer (Arctiidae) (Heitmann, 1934: 180–183), until they finally fill the entire cavity of the thorax, for example in *Heterogynis penella* (Hübner) (Heterogynidae) (Dierl, 1966: 459) and *Erannis defoliaria* (L.) (Geometridae) (Heitmann, 1934: 165). Some reduction of the flight musculature was observed in the brachypterous females of *Agrotis fatidica* (Hübner) and *Ulochlaena hirta* (Hübner) (Noctuidae) (Gohrbandt, 1938: 18) and can be expected whenever the ovaries extend a significant distance into the thorax. It is thus likely that the ability to fly is adversely affected not only by the increasing body weight, which may lead to decreasingly favourable wing loading (i.e. wing: body ratio) and consequently less sustained flight, but also by direct interference of the expanding ovaries with the flight musculature. With decreasing readiness to fly, the trend towards early mating and oviposition

becomes stronger and the females of various species deposit most of their egg complement before the first flight takes place, for example the genus *Setina* Schrank (Arctiidae) (Burmann, 1957, as *Endrosa* Hübner). Continuation of this trend leads eventually to flightlessness and sedentary behaviour with progressive reduction of the wings and legs as observed in families such as Psychidae, Heterogynidae and Lymantriidae and Arctiidae where the females no longer leave the pupation site.

Wing reduction in males

As a result of the division of functions between male and female the sexes have different flight requirements and consequently are subjected to different selective pressures with regard to their flight organs and their ability to fly. This is immediately obvious from the fact that wing reduction rarely occurs in the male. An analysis of those species that are wing-reduced in both sexes shows that they are all inhabitants of mostly small oceanic islands or restricted coastal habitats. The effect of continuous strong winds has long been invoked to explain the high incidence of wing reduction in island insects and provides also the most plausible explanation for brachyptery in Lepidoptera males. The most important activity of the male involving flight is the search for a mate; however, continuous high wind speeds, as they prevail for example on the small sub-Antarctic islands, make directional flight impossible. Individuals attempting to fly will be carried out of their habitat without much chance of regaining it (Gressitt, 1970: 364). Moreover, very strong winds must rapidly disperse the pheromones emitted by a female to such an extent that no pheromone trail would develop for the male to follow. Under such circumstances there would be no attraction over long distances whilst over short distances, for example in the shelter of grass tussocks and other dense, low-growing vegetation, alternative means of locomotion, such as jumping or running, are more effective. In an environment where high wind speeds are the norm a shift from flying to jumping and a reduction of the wing area exposed to the wind becomes advantageous because they increase the ability of the moth to stay in control of its movements. At the same time the reduced wings probably fulfil also an important function as stabilizers during a jump, and the greater need of the male for speed and manoeuvrability in the competitive courtship process may be the reason why the male wings are occasionally less reduced than those of the female. Both male and female sometimes show a tendency towards stenoptery, for example *Exsilirarcha graminea* Salmon & Bradley (Pyralidae) (Fig. 40; Salmon & Bradley, 1956: figs 24, 27), and it is likely that stenopterous wings are more effective stabilizers to a jumping moth than are broader wings. The resistance of the male to flightlessness is so great that even in windswept alpine and arctic habitats no brachyptery has evolved in that sex. Significantly, wing reduction in both sexes of a species restricted to high mountain habitats above the tree line (oreal species) is known only in the two oceanic island species *Thyrocopa apatela* (Walsingham) (Oecophoridae, Xyloryctinae) (Hawaiian Islands, Maui) (Figs 7, 8; Zimmerman, 1978: 937, fig. 560) and *Ephysteris* sp. (Gelechiidae) (Madeira) (Sattler, 1988: 232). It is noteworthy that *Ephysteris curtipennis* (Zerny) (Morocco, High Atlas), which is closely related to the Madeiran species and occurs under similar environmental conditions, has macropterous males (Zerny, 1936: 138). However, the reasons for that difference may be connected with the smaller population and limited size of the habitat on the oceanic island, because a flying male that is removed from its habitat by the force of strong winds is unlikely to find an alternative population as it might in the much larger continental habitat.

Although Salmon (1956: 62) and Viette (1959: 22) accept the strong winds as the prime cause of flightlessness in sub-Antarctic island Lepidoptera, they additionally assume a genetic predisposition to brachyptery. If this were so, one would expect to find some tendency towards wing reduction elsewhere amongst the nearest relatives of such species, particularly where these occur in environments that normally favour brachyptery. One example in support of this view is the genus *Asaphodes* Meyrick (Geometridae) with two brachypterous sub-Antarctic island species, originating from New Zealand stock, and several 'mainland' species, some of them with brachyptery. However, other species on sub-Antarctic and other oceanic islands are clearly the only brachypterous members of large, widespread genera of macropterous species without the tendency towards wing reduction elsewhere in the world (for example *Elachista* Treitschke, *Borkhausenia* Hübner, *Udea* Guenée, *Peridroma* Hübner). Considering all types of wing reduction in the Lepidoptera, and the many different lineages in which brachypterous forms have arisen independently, it appears likely that many species would in time respond in that way to appropriate environmental pressures.

The low temperature on sub-Antarctic islands is sometimes also invoked to explain the reluctance of insects to fly in such habitats. However, the cold cannot account for male flightlessness in the

Lepidoptera, because there are several successful strategies that enable, for example, northern hemisphere winter-active Geometridae and Noctuidae to fly in much lower ambient temperatures, even below freezing. Moreover, several Lepidoptera with male brachyptery occur in high temperature environments, for example *Ambloma brachyptera* Walsingham (Symmocidae) and *Areniscythris brachypteris* Powell (Scythrididae) in coastal sand dunes on the Canary Islands and in California respectively, where other factors must be responsible.

Wing reduction in cold season moths

The largest category with environmentally induced wing reduction in the female sex is that of the northern hemisphere cold season species ('winter moths') which are univoltine and have an adult activity period somewhere between about late October and April. Examples of this category are known in the Eriocottidae, Tineidae, Oecophoridae (Ethmiinae, Chimabachinae), Tortricidae, Somabrachyidae and possibly Lasiocampidae and Arctiidae; they are particularly numerous in the Geometridae (Oenochrominae, Larentiinae, Ennominae). The severe conditions of continental winters usually act as a strict barrier that sharply divides the cold season moths into a 'late' (moths emerging October-December) and an 'early' (moths emerging January-April) group; however, in the mild oceanic winter climate of the British Isles both groups may overlap and blend into each other. Even under extreme low temperatures the break is not always absolute as is demonstrated by *Cheimoptena pennigera* Danilevsky (Geometridae), an inhabitant of the Central Asiatic deserts, with an adult activity period that extends from December till February (see below).

There is so far only moderate evidence of a comparable southern hemisphere cold season element, for example in New Zealand the genus *Atomotricha* Meyrick (Oecophoridae), which has several winter species with adult activity periods in about August-September, and a few diurnal Tortricidae (Dugdale, pers. comm.) and *Zermizinga indocilisaria* Walker (Geometridae; also found in Australia).

A significant minority of the Lepidoptera in the temperate zone of the northern hemisphere pass the cold season as adults, and species overwintering in that stage are known in many families, for example Opostegidae, Gracillariidae, Yponomeutidae, Lyonetiidae, Oecophoridae (Depressariinae), Momphidae, Gelechiidae, Tortricidae, Alucitidae, Pterophoridae, Pyralidae, Pieridae, Nymphalidae and Noctuidae. Because of their longevity both sexes of such species depend on an intake of energy; they have fully developed mouth parts and feed. Many overwintering moths are capable of flying at low ambient temperatures. The importance of flight in the search for food sources, hiding places and oviposition sites acts against flightlessness in such species, and no example of wing reduction in Lepidoptera overwintering as adults is known. Other species are active in autumn and into the colder part of the year (for example *Agrochola* Hübner) or emerge very early in the year but extend their activity period into the warmer months (for example *Orthosia* Ochsenheimer). In common with the overwintering moths these species feed, for example early Noctuidae of the genus *Orthosia* Ochsenheimer at *Salix* catkins, and show no tendency towards flightlessness.

The group in which wing reduction in females has evolved comprises those species that emerge in late autumn, frequently after the first frost, winter or early spring and complete their adult life in the cold season. Both sexes of such species are short-lived; they do not feed and their mouth parts are usually reduced. The males are capable of flying in very low air temperatures, often below 0°C. The females of certain species are fully winged, albeit with a more or less strong tendency towards flightlessness, for example *Semioscopis oculella* (Thunberg), *S. avellanella* (Hübner) (Oecophoridae); *Poecilocampa populi* (L.), *Eriogaster lanestris* (L.) (Lasiocampidae); *Lemonia vallantini* (Oberthür) (Lemoniidae); however, those of most species show various degrees of wing reduction, from brachypterous half-sized wings in *Protalcis* Sato to microptery or aptery in *Erannis* Hübner (Geometridae) (for example Inoue, 1982: pl. 98). They are motile with normal functional legs and are capable of walking, climbing and sometimes running, but they do not jump. The females emerge from pupae on the ground with their egg complement fully developed; those of the flightless species ascend tree trunks, where they soon attract the males and mating takes place. The eggs are then deposited without much delay high up in the canopy of the same trees. As the larvae of most cold season moths are polyphagous, usually on deciduous trees, there is no need for flight in search of an appropriate host-plant on which to lay the eggs, and an important barrier to flightlessness and wing reduction in the female is removed. The female's loss of the ability to disperse is at least in part compensated by a dispersal phase in the larval stage when the young larvae actively migrate from the oviposition site to other parts of the plant or are passively transported through the air, ballooning on silken threads. Such passive transport accounts for the

presence of larvae on isolated bushes or on trees that had been protected from ascending females by sticky bands. The suggestion that the female may be carried to such isolated sites by the male during copulation, a claim often made with reference to the winter moth *Operophtera brumata* (L.) (e.g. Porritt, 1913), was never supported by direct observation and has long been discredited (Chapman, 1913: 81, 1917: 63).

Many cold season moths are nocturnal, for example *Alsophila* Hübner, *Operophtera* Hübner, *Apocheima* Hübner, *Lycia alpina* (Sulzer), *Agriopis* Hübner and *Erannis* Hübner, and their activity frequently begins shortly after sunset; however, several species with more or less fully winged females, for example *Semioscopis oculella* (Thunberg), or brachypterous females, for example *Dasyethmia hiemalis* Danilevsky, *Cheimophila salicella* (Hübner), *Exapate duratella* (Heyden), *Synnoma lynosyrana* Walsingham, *Chondrosoma fiduciarium* Anker, *Lycia zonaria* (Denis & Schiffermüller), *Cheimoptena pennigera* Danilevsky and *Ocnogyna* spp., are diurnal, with the male courtship flight usually taking place in sunshine.

Lepidoptera are capable of flight only within a certain range of ambient temperatures. If the temperature drops below a critical point the insect is no longer able to maintain the minimum thoracic temperature necessary for its flight muscles to operate. In contrast, if the ambient temperature exceeds the critical upper limit, not enough excess heat is discharged to the environment. In either case the duration of the flight is curtailed as the critical temperature is approached until flight ceases altogether. During flight many Lepidoptera are homoeothermic; they have their specific operating temperature which is more or less constant and largely independent of the ambient temperature. For example, the in-flight thoracic temperature of many Noctuidae is maintained at about 30°–35°C (Heinrich, 1987: 319–320, fig. 6) and similar temperatures have been measured in butterflies (Heinrich, 1981: 249). The heat required to reach and maintain the operating temperature of the flight musculature can be generated endothermically by the insect's own metabolism. Many nocturnal Lepidoptera, for example Noctuidae and Sphingidae, raise their thoracic temperature in a mandatory preflight warm-up by a process of 'shivering', i.e. rapid contractions of the flight muscles accompanied by low amplitude wing vibrations (Kammer, 1981: 132–138), but this method of warm-up has not been recorded for the males in any of the cold season species with flightless females. During flight the operating temperature in the thorax is maintained through insulation, which reduces convective heat loss, and a counter-current heat exchange system that diminishes the loss of heat from the thorax to the head and abdomen (Heinrich, 1987).

Field observations on the flight behaviour of some diurnal cold season species (Burmann, 1953, 1965; Danilevsky, 1969*a*, 1969*b*) suggest that they may also be homoeothermic in flight but raise the temperature of their flight musculature to an operational level by acquiring heat ectothermically from solar radiation. It has been argued that the wings act as highly effective solar heat collectors which absorb and transport the energy to the thorax with the aid of haemolymph circulating through the wing veins (Clench, 1966); however, this has been disputed on the grounds that the haemolymph flow is insufficient to be effective (Kammer, 1981: 307). Instead, it has been suggested that warm air accumulates under the wings of basking Lepidoptera (such as dorsal baskers amongst the butterflies) and enables heat exchange with the body by convection (Casey, 1981: 96–99). The latter explanation is also plausible for diurnal moths that maintain a roof-like wing posture during warm-up rather than spread their wings to give them maximum exposure to the sun. The effect of the wings in such a resting position is then that of a greenhouse and is apparently adequate to allow the males of certain cold season species to commence their courtship flight soon after sunrise during the coldest hour of the day. For example, the mating flight of *Semioscopis oculella* (Thunberg) (= *anella* Hübner) (Oecophoridae), a species with a fully winged but almost flightless female, and *Exapate duratella* (Heyden) (Tortricidae), a species with a brachypterous female, begins soon after the sun reaches their habitat, even when the air temperature is still well below freezing (Burmann, 1953, 1965).

In contrast to the homoeothermic species, nocturnal cold season Geometridae are poikilothermic in flight, i.e. their body temperature is variable and depends on the ambient temperature. Because their heat production is low and convective heat loss of their small bodies to the environment is high, their in-flight thoracic temperature is maintained within a few degrees of the ambient temperature (Casey & Joos, 1983). Their low wing loading, i.e. a large wing area in relation to the body mass, permits them to fly at low wing stroke frequencies. Although such flight is slow and poorly controlled it has the advantage that it is instant over a wide range of ambient temperatures, without the mandatory preflight warm-up of species which have a high wing loading and a better flight performance such as Sphingidae and Noctuidae. Most importantly, the energy required to generate the minimum power for lift-off and

flight is low and the flight musculature is able to operate effectively at a low temperature. Consequently, winter moths such as the North American *Alsophila pometaria* (Harrison) and *Operophtera bruceata* (Hulst) are able to sustain themselves in flight at thoracic muscle temperatures as low as −3°C (Heinrich & Mommsen, 1985).

The main selective advantage of a shift of the adult activity period to the cold season is seen in the reduced predator pressure at a time when arthropod predators are dormant, insectivorous mammals in hibernation, migratory insectivorous birds absent and resident populations of birds at low density whilst some of them (for example *Parus* spp.) have switched their diet from insects to seeds (Dierl & Reichholf, 1977: 33–34).

Several hypotheses have been offered to account for the prevalence of wing reduction amongst cold season species. According to Hudson (1912: 274) flightlessness prevents the female from straying so far from the host-plant of its larva that it would be unable to regain it were it overcome by the cold whilst some distance away. Chapman (1917: 62) suggested that the female, once removed from its host-plant, would be unable to locate a substitute by chemical cues ('scent') at a time when the vegetation is leafless and dormant. Hering (1926: 214) argued that the seasonal storms in the northern temperate zone in autumn and spring would carry females out of reach of a suitable oviposition site if they attempted to fly. All three of those explanations see the selective advantage of flightlessness in the cold season in a better chance of the female in finding an oviposition site. However, the selection of such a site is hardly critical enough in this context because the larvae of most cold season species are polyphagous and often have an early dispersal phase that further aids in locating a host-plant. Were flight essential in this process, the problem of low temperatures would have been overcome by the female adopting one of the strategies successfully employed by winter-flying males. The wind factor can hardly be invoked in this case either, because the seasonal storms are never as continuous as, for example, on the sub-Antartic islands so that conditions suitable for flight would exist at least at some time during the normal lifespan of an individual. Were strong winds responsible in the way suggested by Hering, then both sexes would be equally affected because the difficulty of a female in locating a host-plant is no greater than that of a male in finding a mate.

Based on an analysis of the Winter Moth, *Operophtera brumata* (L.) (Geometridae), Dierl & Reichholf (1977) argued that cold season brachyptery is an energy conservation measure that protects the egg-bearing female from excessive loss of heat to a low temperature environment. The larger the wing area in relation to body size, the greater the loss of heat to the environment and the greater obviously the benefits of energy saving through wing reduction. However, as the role of the wings as heat exchangers is disputed and may be negligible (Kammer, 1981: 307) that explanation is not entirely satisfactory and it is more likely that environmental factors other than a low temperature are responsible for cold season wing reduction. To a host-specialist in a stable but patchy environment it is advantageous to be long-lived and motile because that increases its chances of locating a scarce, scattered food resource on which to deposit its eggs. In contrast, under unpredictable environmental conditions, as they prevail during the cold season with sudden drastic weather changes, it must be of selective advantage if the vulnerable adult stage is short. This presupposes that the female is instantly ready for mating and ovipositing when environmental cues, for example temperature, humidity or barometric pressure, signal favourable ambient conditions and trigger its emergence from the pupa. But, as discussed on p. 250, the entire mature egg complement can only be accommodated simultaneously if the ovaries are extended more or less far forward into the thorax, where they interfere with the flight musculature and thus cause flightlessness. In such circumstances it is of advantage to the female to shed the burden of the wings, over which it has diminished control, and redirect the energy saved into egg development.

Wing reduction in oreal moths

Another group with a high incidence of wing reduction in the female sex is that of the oreal species, i.e. species that inhabit high mountains above the tree line. Oreal species with brachypterous females are found in the Hepialidae, Tineidae, Yponomeutidae, Blastobasidae, Symmocidae, Gelechiidae, Lecithoceridae, Tortricidae, Pyralidae, Geometridae, Arctiidae and Noctuidae. Most of the known species occur in the Palaearctic region (Atlas mountains, European mountains, Central Asian mountains), a small number in tropical Africa (Kilimanjaro, Ruwenzori), South America (Andes), Australia and New Zealand. Unspecified high altitude Gelechiidae were recorded from North America (Colorado Rocky Mountains) (Hodges, 1986: 6) and further discoveries in this category, particularly amongst the Microlepidoptera, can be expected in various parts of the world in poorly explored alpine habitats. For example, several as yet unidentified

strongly brachypterous females, including some Blastobasidae, were recently collected by Karsholt in the Peruvian Andes at altitudes of 3500–4300 m.

Thyrocopa apatela (Walsingham) (Oecophoridae, Xyloryctinae), endemic to the Hawaiian island of Maui (Figs 7, 8; Zimmerman, 1978: 937, fig. 650), and an undescribed *Ephysteris* species (Gelechiidae), endemic to the Atlantic island of Madeira (Sattler, 1988: 232), inhabit oreal habitats but are brachypterous in both sexes (see p. 251).

The brachypterous females of oreal species are usually motile; they are able to walk and run, for example *Agrotis fatidica* (Hübner) (Noctuidae), and often also jump, for example *Kessleria* Nowicki (Yponomeutidae), *Thyrocopa apatela* (Walsingham) (Oecophoridae, Xyloryctinae) (both sexes), *Caryocolum laceratella* (Zeller), *Sattleria* Povolný (Gelechiidae) and *Sphaleroptera alpicolana* (Frölich) (Tortricidae). In some species the mouth parts are sufficiently well developed that they might be functional; however, neither sex of such species was ever observed on flowers or other potential food sources and it is likely that feeding, if it takes place, is restricted to the intake of water to counteract desiccation.

Some authors have compared flightlessness in oreal species to the same phenomenon in cold season species on the grounds that the adults of both groups may be exposed to very low temperatures (Hudson, 1912: 273; Dierl & Reichholf, 1977: 30). However, an important difference with regard to the temperature factor is that the cold season species must be able to operate in very low ambient temperatures whilst the adults of most oreal species are summer-active, when conditions allow flight within a temperature range that is normal for Lepidoptera. Thus various nocturnal oreal species fly only when it is relatively warm, and their flight ceases well above the freezing point. Nevertheless many oreal species are diurnal. The males of several species with wing-reduced females fly in the sunshine and cease flying as soon as the sun is obscured by clouds, for example *Pharmacis pyrenaicus* (Donzel) (Hepialidae) and *Sphaleroptera alpicolana* (Frölich) (Tortricidae) (pers. obs.). In common with the males of some diurnal winter moths those of several oreal species such as *Acompsia dimorpha* Petry (Gelechiidae) (Petry, 1904: 6) and *Sphaleroptera alpicolana* (Frölich) (Tortricidae) (Burmann, 1958: 1) commence their courtship flight early in the morning when they probably absorb the rays of the rising sun for a preflight warm-up. Having ruled out exposure to low temperatures as critical, the common factor that links oreal species with cold season species is seen here in an uncertain environment. Even in summer the alpine zone of high mountains is often subjected to strongly fluctuating weather conditions, not unlike those in the cold season, sometimes with sudden snowfall, which would favour short-lived species with their potential for wing reduction in the female.

It should be noted that there are some oreal cold season species. *Lycia alpina* (Sulzer) (Geometridae), which occurs in the European Alps at altitudes of about 1500–2500 m, is the first moth to emerge along the edges of the receding snow from late April till mid-July, depending on the altitude and exposure of the habitat to the sun. Like the males of other true cold season species those of *L. alpina* are crepuscular to nocturnal and fly at ambient temperatures around freezing point (Pinker, 1953: 179; Burmann, 1956). It can be assumed that in common with other cold season Geometridae they operate at thoracic temperatures near the ambient temperature whilst most other oreal species can be expected to have a high operating temperature. *L. alpina* is closely related to other cold season species such as *L. zonaria* (Denis & Schiffermüller) and *L. pomonaria* (Hübner) which are restricted to lower altitudes, but whilst the adults of the lowland species are active at a time of lowest predator pressure (Dierl & Reichholf, 1977: 33–35), those of oreal species such as *L. alpina* emerge after the arrival of the migratory birds and sometimes suffer from heavy bird predation (Pinker, 1953: 179; Burmann, 1956: 256).

Flight in a high temperature environment

Having established that certain environmental conditions can induce wing reduction and having identified strong winds on small oceanic islands and sudden weather changes in the cold season or in oreal habitats as potential factors, it is worth considering whether other extreme or unusual environmental factors could have a similar effect. Although low temperature was rejected as a significant factor, it is imaginable that an extreme high temperature environment could favour the evolution of wing reduction because in a high ambient temperature moths would not be able to discharge into the environment enough of the excess heat generated by their flight musculature. Consequently their flight would be curtailed and eventually cease altogether, particularly in the heavier female sex, and such enforced flightlessness could give rise to wing reduction. However, most of the summer-active species with wing-reduced females occur in the temperate regions where temperatures do not consistently rise for any significant length of time above the critical levels beyond which Lepidoptera are no longer

able to fly. Although much still remains to be discovered in the tropics, there is as yet no evidence of wing reduction linked to high temperature.

Wing reduction in forest moths

A number of Lepidoptera with wing-reduced females, including Psychidae, Oecophoridae, Tortricidae, Geometridae and Lymantriidae, are inhabitants of northern hemisphere broad-leaved forests. According to Barbosa *et al.* (1989), who investigated forest-dwelling Lepidoptera in eastern North America, flightlessness in such species arose as a response to ecological pressures from the forest environment. Although forests provide favourable conditions for flightless species because they constitute a permanent, continuous habitat with stable food sources, an analysis of forest-inhabiting wing-reduced species indicates that the factors critical for the evolution of flightlessness and wing reduction may not be inherent in the specific ecological conditions of the forest environment.

Flightlessness is a family strategy in Psychidae (p. 262) and is common in Lymantriidae (p. 277). Thus it is likely that the affected forest-dwelling species in these families evolved from ancestors that were already flightless when entering the forest environment. In contrast, flightlessness and wing-reduction in Geometridae, Oecophoridae and Tortricidae may have evolved in the forest; however, all the forest-inhabiting wing-reduced members of those families are cold season species for which unpredictable seasonal weather conditions are seen as the critical evolutionary factor (p. 254).

Wing reduction in steppe and desert moths

Some instances of brachyptery have been interpreted as a response to environmental conditions in steppes and deserts. Zerny & Beier (1936: 1568) suggested that in xerothermic habitats the female would be unable to locate suitable plants for oviposition at times when flowers and leaves were dried up. Under such circumstances it would be advantageous if the female were prevented from straying too far from the host-plant of its own larva. However, there is no evidence of an increased incidence of brachyptery in steppe and desert Lepidoptera to suggest an inherent factor favouring the evolution of wing reduction in that environment. Moreover, the examples given by Zerny & Beier can be interpreted more convincingly by other factors; *Somabrachys* Kirby (Somabrachyidae), *Lambessa* Staudinger (= *Lasiocampa* Schrank) (Lasiocampidae) and *Ocnogyna* Lederer (Arctiidae) are cold season forms whereas wing reduction in summer-active *Chondrostega* Lederer (Lasiocampidae) is the result of sedentary habit.

Wing reduction in aquatic moths

A number of Lepidoptera, mostly Pyralidae of the subfamily Nymphulinae, have adapted to an aquatic way of life with their larvae living on or in the submerged parts of water plants. However, the adults of all species leave the water and are capable of flying with the exception of a female morph of *Acentria ephemerella* (Denis & Schiffermüller), which remains submerged throughout its adult life and has reduced wings adapted for swimming (see p. 274). It is obvious that any shift of the adult stage from air into water would require significant modification of the wings including a reduction in their size.

Flightlessness in cavernicoles

Wing reduction is one of the morphological adaptations characteristic of many obligate cavernicoles amongst the insects (Howarth, 1983: 374) but is so far unknown in cave-dwelling Lepidoptera. Many cavernicolous Lepidoptera are probably at best troglophiles, i.e. species with permanent cave-dwelling populations which also occur above the ground in comparable microhabitats, whilst the number of troglobites, i.e. species which complete their life cycle in caves and are unable to survive outside the hypogaean environment, is very small. As the larvae of most Lepidoptera depend for their food on the live tissue of green plants, most species with permanent cave-dwelling populations are members of the tineid subfamily Tineinae, the larvae of which utilize as their energy source various kinds of animal detritus such as bird and bat guano and associated arthropod remains. The habits and distribution of many cavernicolous Tineidae are still inadequately known and it is difficult to establish their ecological status; however, at least one species, *Tinea microphthalma* Robinson from the Philippines, has significantly reduced eyes typical of true troglobites but is macropterous in the male whilst the female is still unknown (Robinson, 1980: 111, figs 35, 47). Another group of troglobitic Lepidoptera are species of the genus *Schrankia* Hübner (Noctuidae) inhabiting lava tubes in the Hawaiian Islands. Lava tubes are frequently so close to the surface that they can be invaded by the roots of native trees such as *Metrosideros polymorpha* (Myrtaceae) (Howarth, 1973: 144, fig. 1) which are the food source for the *Schrankia* larvae. Whilst *Schrankia* males are weak fliers, the females,

which are usually found near their cocoons, are flightless but not appreciably wing-reduced (Howarth, 1983: 376).

Flightlessness in a butterfly inhabiting the communal nest of its larvae

Geiger *et al.* (1989: 32) recently recorded an interesting case of incipient wing reduction in the Mexican *Eucheira socialis* Westwood (Pieridae) resulting from the unusual biology of this species. Its gregarious larvae spin large communal nests from which they emerge only for nocturnal feeding and in which they eventually pupate. Whilst the adults of *E. socialis westwoodi* Beutelspacher from the north-western part of central Mexico leave the shelter and are capable of weak flight, those of *E. socialis socialis* from southern Mexico cannot fly at all and remain permanently in the nest where they mate and oviposit. According to Geiger *et al.* most females lay only a few eggs, thus obviating the need for feeding in order to acquire energy from external sources for additional egg production. Populations are only sustainable at such low reproduction rates if excessive losses from predation, parasitism or unfavourable environmental conditions can be prevented; therefore it may be assumed that the communal nests in conjunction with the nocturnal feeding habit of the larvae provide adequate protection. Although the wings of the adults appear to be full size, Geiger *et al.* observed some reduction of the venation in the female and it is easy to visualize how, with time, brachyptery could evolve under the special conditions of nest-living. Almost certainly wing reduction in this instance would not be confined to the female but would also affect the male; in other groups of Lepidoptera wing reduction occurring in both sexes of a species has arisen only under the influence of strong winds.

E. socialis demonstrates that loss of flight can evolve in butterflies and that there is even potential for wing reduction. Nevertheless, butterflies are a group that offers poor candidates because, in many species, a mate-locating system involving active participation of the male and female is an effective barrier against the evolution of flightlessness in either sex. Other aspects of butterfly biology provide similarly effective barriers. For example, in some *Heliconius* species (Nymphalidae, Heliconiinae) males are attracted to female pupae which they guard until they are able to mate with the freshly emerge female (Gilbert, 1976: 420). However, as the female does not leave the pupa with a fully developed egg complement it must retain its ability to fly in search of food sources in order to produce energy for further egg development. Moreover, host-specificity of the larvae, which requires more or less extensive searches for oviposition sites, makes further demands on the motility of the female.

Flight in Saturniidae

It is surprising that there is no record of flightlessness in females of Saturniidae, many species of which appear to be singularly pre-adapted to loss of flight and even wing reduction. Adult Saturniidae are short-lived and do not feed; most species have non-functional, reduced mouthparts. The female emerges from the pupa with its total egg complement fully developed and thus is instantly ready to mate and oviposit. Effective long-ranging pheromones guide the male to the female so that the latter does not have to participate actively in the mate-locating process. As the larvae of many species are polyphagous, oviposition can take place unselectively without flight playing a critical role in the search for oviposition sites. The saturniid wings with bright warning coloration suggest that such species are unpalatable and thus enjoy some protection from diurnal vertebrate predators without having to resort to flying as a means of escape. Conspicuous eye spots on the wings of many species fulfil a similar defensive role. Consequently there appears to be no necessity for the females to fly for purposes of feeding, mate-finding, ovipositing or escaping from predators and one might therefore have expected some tendency towards wing reduction or at least sedentary behaviour; however, no evidence of this has been found. The females of Saturniidae have succeeded in retaining their ability to fly by avoiding the loss of flight musculature and maintaining a sufficiently low wing loading. To accommodate a large egg complement the volume of the abdomen has been greatly increased thus obviating the need to extend the ovaries forward into the thoracic cavity where, in many flightless Lepidoptera, they displace the flight musculature. The consequent problem of wing loading, which would be adversely affected by an increasing body weight, has been solved by enlargement of the wing area, and it is probably no coincidence that most Saturniidae are very large moths. It is not clear at this stage what kinds of selective pressure have prevented flightlessness in Saturniidae and it is interesting to note that wing reduction did evolve under apparently similar conditions in certain Lasiocampidae, Lymantriidae and Arctiidae.

Check list of family-group taxa in which wing reduction occurs

Wing reduction is usually restricted to the female sex; taxa in which it is recorded in both sexes are marked with an asterisk (*).

HEPIALOIDEA
  Hepialidae
TINEOIDEA (*)
  Eriocottidae
  Psychidae
  Tineidae (*)
YPONOMEUTOIDEA (*)
  Yponomeutidae (*)
  Glyphipterigidae
GELECHIOIDEA (*)
  Oecophoridae (*)
    Depressariinae
    Ethmiinae
    Xyloryctinae (*)
    Oecophorinae (*)
    Chimabachinae
  Elachistidae (*)
  Blastobasidae
  Symmocidae
  Cosmopterigidae
  Gelechiidae (*)
    Aristoteliinae
    Gelechiinae (*)
      Gnorimoschemini (*)
    Anacampsinae
  Lecithoceridae
  Scythrididae (*)
TORTRICOIDEA (*)
  Tortricidae (*)
    Tortricinae (*)
    Olethreutinae
ZYGAENOIDEA
  Heterogynidae
  Zygaenidae
    Procridinae
  Somabrachyidae
COPROMORPHOIDEA (*)
  Carposinidae (*)
PYRALOIDEA (*)
  Pyralidae (*)
    Pyralinae
    Crambinae
    Acentropinae
    Pyraustinae (*)
    Scopariinae (*)
GEOMETROIDEA
  Geometridae
    Oenochrominae
    Ennominae
      Semiothisini
      Bistonini
      Gnophini
    Larentiinae
      Xanthorhoini
      Operophterini
BOMBYCOIDEA
  Lasiocampidae
NOCTUOIDEA (*)
  Lymantriidae
  Arctiidae
    Lithosiinae
    Arctiinae
    Ctenuchinae
  Noctuidae (*)
    Acronictinae
    Cuculliinae
    Hadeninae
    Noctuinae (*)

Check list of the Microlepidoptera species, including Pyralidae, with wing reduction

An attempt is made to list all species of Microlepidoptera, including the Pyralidae, in which wing reduction is known. Species with merely slight sexual wing dimorphism that may be an indication of the beginning of wing reduction in the female are excluded. The species of Psychidae, Heterogynidae and Somabrachyidae are not individually listed because most or all members of those families are affected. As far as possible the taxa are arranged in a systematic sequence. The valid name of each species is followed by an indication of the wing-reduced sex (a sex symbol in square brackets indicates that an as yet unknown sex is likely to be wing-reduced) and the general area of distribution. For oreal species the mountain range is added in parentheses and for oceanic island species the island group. Northern hemisphere cold season species are identified by the months of their adult activity period given in Roman numerals in parentheses.

Hepialidae

Pharmacis pyrenaicus (Donzel, 1838) ♀ Europe (Pyrenees)
Pharmacis anselminae (Teobaldelli, 1977) ♀ Europe (Alps)
Pharmacis bertrandi (Le Cerf, 1936) ♀ Europe (Alps)
Aoraia senex (Hudson, 1908) ♀ New Zealand (1100–1700 m)
Aoraia species ♀ New Zealand (1100–1500 m)

Eriocottidae

Deuterotinea auronitens Lucas, 1956 [♀] Morocco (xi)
Deuterotinea axiurga (Meyrick, 1922) [♀] Syria (?)
Deuterotinea balcanica Zagulajev, 1972 [♀] Bulgaria (xi-i)
Deuterotinea casanella (Eversmann, 1844) ♀ South Russia (ix, x)
Deuterotinea instabilis (Meyrick, 1924) [♀] Cyprus (xii-iii)
Deuterotinea maracandica Zagulajev, 1988 [♀] Uzbekistan (?)
Deuterotinea palaestinensis Rebel, 1901 [♀] Israel (?)

Deuterotinea paradoxella (Staudinger, 1859) ♀ Spain (xi-i)
Deuterotinea stschetkini Zagulajev, 1972 ♀ Turkmeniya, Tadzhikistan (xi)

Psychidae
Most species ♀ World-wide

Tineidae
Tinea allomella Bradley, 1965 ♀ East Africa (Ruwenzori)
Eudarcia brachyptera (Passerin d'Entrèves, 1974) ♀ Italy
Eudarcia gallica (Petersen, 1962) ♀ Europe, France
Pringleophaga crozetensis Enderlein, 1905 ♂, ♀ South Indian Ocean (Crozet Is)
Pringleophaga kerguelensis Enderlein, 1905 ♂, ♀ South Indian Ocean (Kerguelen Is)
Pringleophaga marioni Viette, 1968 ♂, ♀ South Indian Ocean (Marion I.)
Proterodesma turbotti (Salmon & Bradley, 1965) ♂, ♀ South Pacific (Antipodes Is, Bounty I.)
Pararhodobates syriaca (Lederer, 1857) ♀ Central Asia – China (x, i-iv)

Yponomeutidae
Kessleria zimmermanni Nowicki, 1864 ♀ Europe (Carpathians)
Kessleria species ♀ Europe (Alps)
Kessleria pyrenaica Friese, 1960 ♀ Europe (Pyrenees)
Embryonopsis halticella Eaton, 1875 ♂, ♀ South Indian Ocean (Kerguelen Is)

Glyphipterigidae
Glyphipterix rugata Meyrick ♀ New Zealand

Oecophoridae
Depressariinae
Proteodes clarkei Philpott, 1926 ♀ New Zealand
Ethmiinae
Ethmia discrepitella (Rebel, 1901) ♀ U.S.S.R., southern Ural (iv-v)
Ethmia charybdis Powell, 1973 ♀ U.S.A., California (xi-xii)
Dasyethmia hiemalis Danilevsky, 1969 [♀] U.S.S.R., Kazakhstan (i)
Xyloryctinae
Thyrocopa apatela (Walsingham, 1907) ♂, ♀ Pacific Ocean (Hawaiian Is, Maui, 3000–4000 m)
Oecophorinae
Borkhausenia falklandensis Bradley, 1965 ♂, ♀ South Atlantic (Falkland Is)
Tinearupa sorenseni sorenseni Salmon & Bradley, 1965 ♂, ♀ South Pacific (Campbell I.)
Tinearupa sorenseni aucklandica Dugdale, 1971 ♂, ♀ South Pacific (Auckland Is)
Chersadaula ochrogastra Meyrick, 1923 ♀ New Zealand
Atomotricha ommatias Meyrick, 1884 ♀ New Zealand
Atomotricha chloronota Meyrick, 1914 ♀ New Zealand
Atomotricha sordida (Butler, 1877) ♀ New Zealand
Atomotricha oeconoma Meyrick, 1914 ♀ New Zealand
Atomotricha versuta Meyrick, 1914 ♀ New Zealand
Pleurota marginella (Denis & Schiffermüller, 1775) ♀ South-eastern Europe
Chimabachinae
Diurnea fagella (Denis & Schiffermüller, 1775) ♀ Europe (iii-v)
Diurnea phryganella (Hübner, 1796) ♀ Europe (x-xi)
Diurnea issikii Saito, 1979 ♀ Japan (iv)
Diurnea cupreifera (Butler, 1879) ♀ Japan (iii-iv)
Diurnea soljanikovi Lvovsky, 1986 [♀] East Asia (iv)
Cheimophila salicella (Hübner, 1796) ♀ Europe (iv)
Cheimophila kurentzovi Lvovsky, 1990 [♀] East Asia (v)
Cheimophila fumida (Butler, 1879) ♀ East Asia (iii-iv)

Elachistidae
Biselachista brachypterella Klimesch, 1990 ♀ Europe (Alps)
Elachista galatheae galatheae (Viette, 1954) ♂, ♀ South Pacific (Campbell I.)
Elachista galatheae antipodensis (Dugdale, 1971) ♂, ♀ South Pacific (Antipodes Is)
Elachista hookeri (Dugdale, 1971) ♂, ♀ South Pacific (Auckland Is)
Elachista pumila (Dugdale, 1971) ♂, ♀ South Pacific (Auckland Is)
Elachista holdgatei (Bradley, 1965) ♂, ♀ South Atlantic (Falkland Is)

Blastobasidae
Unidentified taxon ♀ South America, Peru (Andes)

Symmocidae
Symmoca (*Parasymmoca*) *profanella* (Zerny, 1936) ♀ North Africa, Morocco (Haut Atlas)
Symmoca (*Symmoca*) *signella* (Hübner, 1796) ♀ Europe (Alps)
Ambloma brachyptera Walsingham, 1908 ♂, [♀] Atlantic Ocean (Canary Is)

Cosmopterigidae
Vulcaniella extremella (Wocke, 1871) ♀ Southern Europe

Gelechiidae
Aristoteliinae
Megacraspedus dolosellus (Zeller, 1839) ♀ Europe
Megacraspedus separatellus (Fischer von Roeslerstamm, 1843) ♀ Europe
Megacraspedus subdolellus Staudinger, 1859 ♀ Europe
Megacraspedus lanceolellus (Zeller, 1850) ♀ Europe
Megacraspedus monolorellus Rebel, 1905 ♀ Turkey (Erciyas Dagi)
Megacraspedus binotellus (Fischer von Roeslerstamm, 1843) ♀ Europe
Megacraspedus imparellus (Fischer von Roeslerstamm, 1843) ♀ Europe
Megacraspedus culminicola Le Cerf, 1932 ♀ North Africa, Morocco (Moyen Atlas)
Daltopora felixi Povolný, 1979 ♀ Mongolia
Eulamprotes libertinella (Zeller, 1872) ♀ Europe (Alps)
Gelechiinae (Gnorimoschemini)
Kiwaia glaucoterma (Meyrick, 1911) ♀ New Zealand
Kiwaia jeanae Philpott, 1930 ♂, ♀ New Zealand
Kiwaia plemochoa (Meyrick, 1916) ♀ New Zealand
Gnorimoschema elbursicum Povolný, 1984 ♀ Iran (Elburz Mts)
Paraschema detectendum Povolný, 1990 ♀ South America, Bolivia (Andes)
Ephysteris curtipennis (Zerny, 1936) ♀ North Africa, Morocco (Haut Atlas)
Ephysteris species ♂, ♀ Atlantic Ocean (Madeira, 1400 m)

Ephysteris kasyi Povolný, 1968 ♀ Afghanistan (Dasht-i-Newar, 3000 m)
Caryocolum laceratella (Zeller, 1868) ♀ Europe (Alps)
Sattleria arcuata Pitkin & Sattler, 1991 ♀ Europe (Pyrenees)
Sattleria pyrenaica (Petry, 1904) ♀ Europe (Pyrenees; Basses Alpes)
Sattleria angustispina Pitkin & Sattler, 1991 ♀ Europe (Pyrenees)
Sattleria breviramus Pitkin & Sattler, 1991 ♀ Europe (Alps)
Sattleria melaleucella (Constant, 1865) ♀ Europe (Alps)
Sattleria basistrigella (Müller-Rutz, 1934) ♀ Europe (Alps)
Sattleria styriaca Pitkin & Sattler, 1991 ♀ Europe (Alps)
Sattleria dzieduszyckii (Nowicki, 1864) ♀ Europe (Carpathians)
Anacampsinae
Acompsia dimorpha Petry, 1904 ♀ Europe (Pyrenees)
Stomopteryx mongolica Povolný, 1975 ♀ Mongolia

Lecithoceridae
Ceuthomadarus viduellus Rebel, 1903 ♀ South-eastern Europe
Ceuthomadarus rungsi (Lucas, 1937) [♀] North Africa, Morocco (Atlas Mts)
Ceuthomadarus atlantis Gozmány, 1978 ♀ North Africa, Morocco (Atlas Mts)
Ceuthomadarus funebrella (Chrétien, 1922) ♀ North Africa, Morocco (Atlas Mts)
Ceuthomadarus naumanni Gozmány, 1987 [♀] Afghanistan (Nuristan, 2500 m)
Tegenocharis species ♀ Nepal (Himalaya)

Scythrididae
Areniscythris brachypteris Powell, 1976 ♂, ♀ U.S.A., California

Tortricidae
Tortricinae
Sorensenata agilitata Salmon & Bradley, 1956 ♂, ♀ South Pacific (Campbell I.)
Exapate congelatella (Clerck, 1759) ♀ Europe (x-xi)
Exapate duratella (Heyden, 1864) ♀ Europe, Alps (x-xi)
Oxypteron impar Staudinger, 1871 ♀ South-eastern Europe, Asia Minor (ix-x)
Oxypteron homsana (Amsel, 1954) [♀] Syria, Jordan (xi-xii)
Oxypteron exiguana (de la Harpe, 1860) ♀ Southern Europe, North Africa
Sphaleroptera alpicolana (Frölich, 1830) ♀ Europe (Alps, Pyrenees)
Synnoma lynosyrana Walsingham, 1879 ♀ South-western U.S.A. (x-xi)
Olethreutinae
Olethreutes orestera Bradley, 1965 ♀ East Africa (Ruwenzori)

Heterogynidae
Heterogynis Rambur, all species ♀ Southern Europe, North Africa

Zygaenidae
Procridinae
Pollanisus calliceros Turner, 1926 ♀ Australia (New South Wales, Tasmania; mountains)

Somabrachyidae
Somabrachys Kirby, all species ♀ North Africa - Syria (ix-xi)

Carposinidae
Campbellana attenuata Salmon & Bradley, 1956 ♂, ♀ South Pacific (Campbell I.)

Pyralidae
Pyralinae
Synaphe punctalis (Fabricius, 1775) ♀ Europe, North Africa
Synaphe amuralis (Hampson, 1900) ♀ East Asia
Synaphe bombycalis (Denis & Schiffermüller, 1775) ♀ Europe
Synaphe moldavica (Esper, 1794) ♀ Europe
Synaphe oculatalis (Ragonot, 1885) ♀ Spain, North Africa, Jordan
Crambinae
Catoptria digitella (Herrich-Schäffer, 1849) ♀ Europe (Pyrenees)
Catoptria biformella (Rebel, 1893) ♀ South-eastern Europe (mountains)
Catoptria majorella (Drenowski, 1925) ♀ South-eastern Europe (mountains)
Orocrambus crenaeus (Meyrick, 1885) [♀] New Zealand (mountains)
Orocrambus lindsayi Gaskin, 1975 ♀ New Zealand (Mount Ida)
Kupea electilis Philpott, 1920 [♀] New Zealand (coastal)
Crambus reductus Viette, 1959 ♀ South Indian Ocean (Amsterdam I.)
Acentropinae
Acentria ephemerella (Denis & Schiffer-müller, 1775) ♀ Europe, North America
Pyraustinae
Udea hageni Viette, 1952 ♂, [♀] South Atlantic (Tristan da Cunha)
Scopariinae
Exsilirarcha graminea Salmon & Bradley, 1956 ♂, ♀ South Pacific (Auckland Is, Campbell I.)
Protyparcha scaphodes Meyrick, 1909 ♀ South Pacific (Auckland Is)

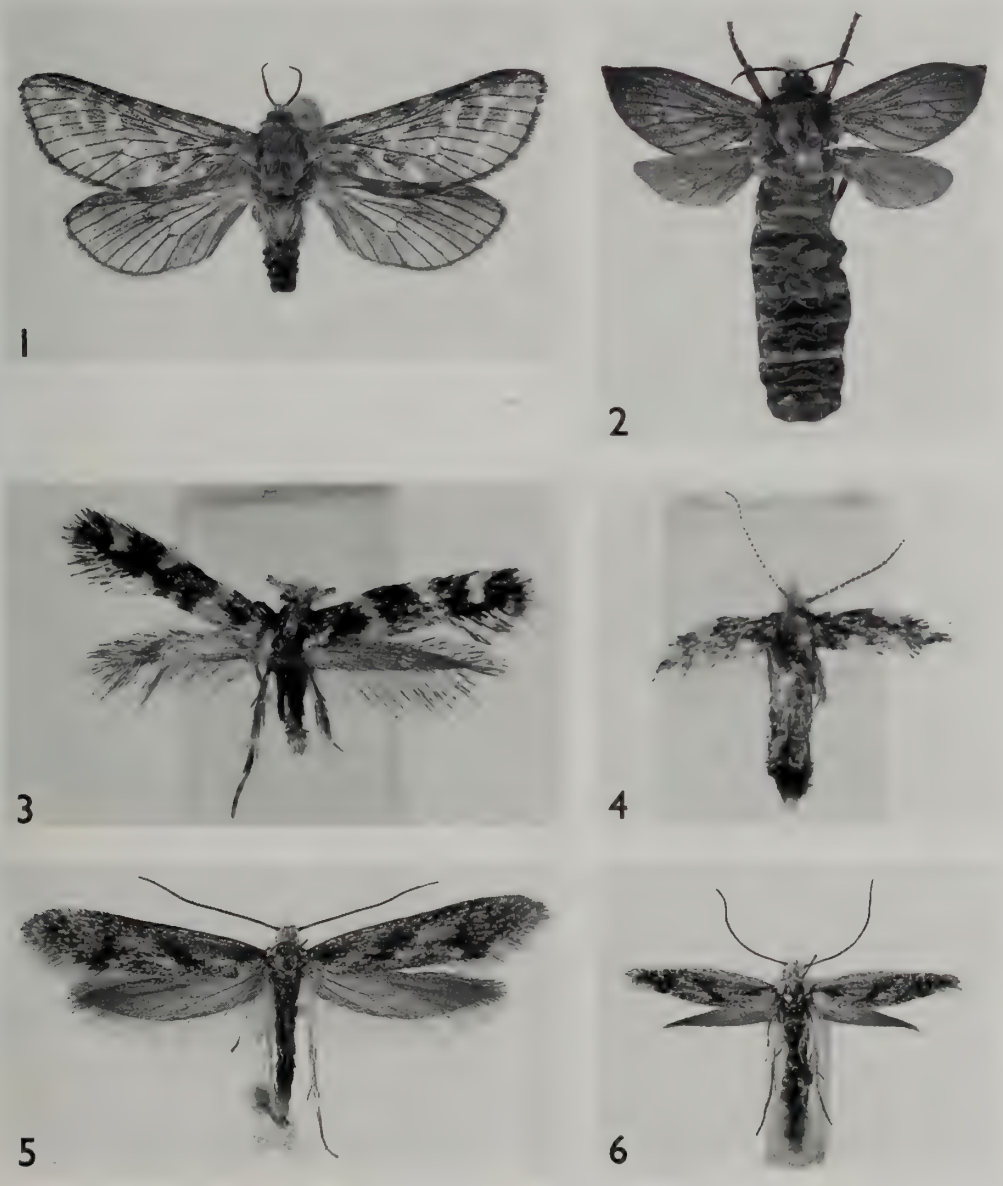
DISCUSSION OF WING REDUCTION IN DIFFERENT FAMILIES

Hepialoidea

1. Hepialidae

The Hepialidae are the only non-ditrysian family of Lepidoptera with examples of wing reduction. Slight to moderate reduction is recorded in the females of two oreal *Aoraia* species occuring in the alpine zone of New Zealand's South Island at altitudes of about 1100–1700 m: *A. senex* (Hudson)

(Dumbleton, 1966: 935) and an undescribed species (Patrick, 1989: fig. 3). Distinct brachyptery has evolved in the females of three oreal *Pharmacis* species (Figs 1, 2; Teobaldelli, 1977: fig. 1; Freina & Witt, 1990: pl. 9) in European mountains (Pyrenees, Alps). *Pharmacis* males are diurnal and fly in the sunshine close to the ground in search of 'calling' females (pers. obs. on *P. pyrenaicus* (Donzel); Teobaldelli, 1977: 41, on *P. anselminae* (Teobaldelli)). Mate-finding by the male is very widespread in the Lepidoptera and appears to be almost universal in nocturnal species; however, in some Hepialidae, for example *Hepialus humuli* (Linnaeus) and *Phymatopus hecta* (Linnaeus), the males form courtship groups at dusk to which the females are visually and chemically attracted (Mallet, 1984; Wagner, 1985). It is evident that brachyptery could not have evolved in species in which the females participate actively in the process of mate locating.



Figs 1–6 1, 2, *Pharmacis pyrenaicus* (Hepialidae), Pyrenees, (1) male, (2) female. 3, 4, *Eudarcia brachyptera* (Tineidae), Italy, (3) male, (4) female. 5, 6, *Kessleria* sp. (Yponomeutidae), Austrian Alps, (5) male, (6) female.

Tineoidea

2. Eriocottidae

In the small family Eriocottidae wing reduction is restricted to the female sex of the Mediterranean to central Asiatic genus *Deuterotinea* Rebel with about 10 nominal species of partly uncertain taxonomic status. The habits of *Deuterotinea* larvae are still unknown but the adults are winter moths (November-March). It can be expected that all species have strongly brachypterous or apterous females although this can only be demonstrated for *D. casanella* (Eversmann) (specimens in BMNH; Zagulajev, 1988: fig. 200), *D. paradoxella* (Staudinger) (Zerny, 1927: 486) and *D. stschetkini* Zagulajev (Zagulajev, 1988: fig. 207). In contrast to all other evidence, Joannis (1917: 260) recorded the adults of *paradoxella* (apparently the males only) as having been collected in June and July.

3. Psychidae

With about 2000 species and an almost world-wide distribution, the Psychidae are the only large family of the Lepidoptera which has adopted flightlessness and wing reduction in the female as a successful family strategy. The loss of locomotion (walking and flying) in the female is so widespread that it must have evolved early in the history of that family. Even the macropterous females of primitive species are often more or less sedentary and a strong tendency towards flightlessness may be a groundplan character of the Psychidae.

The larvae of the Psychidae produce cases which are often clad with plant fragments and other organic or inorganic debris such as lichens, mollusc shells or sand grains. Many species are scavengers or lichen-feeders whilst others are polyphagous on a wide range of green plants. Pupation takes place in the larval case and on ecdysis the pupal exuviae of most species are protruded from the posterior end of the case. With the exception of some primitive species the females are brachypterous or apterous and usually sedentary; their mouthparts and often also the legs and antennae are strongly reduced. When the females emerge from the pupa their egg complement is fully developed, and mating, followed by oviposition, is instantaneous; however, there is also widespread parthenogenesis. The female rarely strays far from the case and inserts its eggs with the aid of a long ovipositor into cracks and crevices nearby or, more frequently, directly into the larval case or pupal exuviae. The ability to deposit the eggs near or into the larval/pupal case immediately after eclosion removes the selective pressure in favour of motility from the female and is a precondition for the reduction of wings and legs. The female's loss of dispersability is successfully compensated by dispersal mechanisms in the larval stage (for a discussion of dispersal in Psychidae see Davis, 1964: 7–8).

According to Saigusa (1962) the single most important factor in the evolution of wing reduction in the Psychidae is the presence of a larval/pupal case. As the females are preadapted to laying eggs into deep cracks with the aid of their long ovipositor the case provides a convenient alternative receptacle for the egg batch. Saigusa identified four stages of reduction of the female's locomotory organs but stated that different degrees of reduction may have evolved independently more than once within the Psychidae. See also Dierl (1973).

(a) The female has fully developed functional wings and legs but the moth is frequently sedentary. It lays its eggs amongst mosses, into crevices in rocks or sometimes into the larval/pupal case.

(b) The female has strongly reduced wings. The legs are developed but are used only for ascending the side of the larval/pupal case. The eggs are laid into the case.

(c) The female has strongly reduced wings and somewhat reduced legs. The moth emerges fully or in part from the pupa and clings to the outer surface of the larval/pupal case near the posterior opening. The pupa is no longer protruded from the case on ecdysis and the eggs are laid into the pupal exuviae.

(d) The female is apterous; its non-functional legs are strongly reduced and lack tarsal claws. The moth remains partially or completely inside the pupa, which is not protruded from the case. A sex attractant is produced by the female from a dorsal hypodermal glandular area (meso- and metathorax, abdominal tergite 1) and is released through a corresponding rupture zone in the pupal skin (Dierl, 1973). The ovipositor is short and the eggs are laid into the pupal exuviae.

4. Tineidae

In the Tineidae wing reduction is rare. Strong reduction of the wings in both sexes occurs in the three species of *Pringleophaga* Enderlein on islands of the sub-Antarctic Kerguelen faunal province (Fig. 59; Crafford *et al.*, 1986: 68, figs 54–88). *Proterodesma turbotti* (Salmon & Bradley) on New Zealand's Antipodes Islands is also strongly brachypterous in both sexes (Salmon & Bradley, 1956: 65, fig. 7) whereas *P. byrsopola* Meyrick is macropterous in New Zealand but shows slight wing reduction on Auckland Island (Dugdale, 1971: 153).

The Asiatic *Pararhodobates syriaca* (Lederer) (Ural and Syria – north-east China) is a winter

moth (October, January-April) with a strongly brachypterous female (Zagulajev, 1975: 162, figs 87, 88). *Tinea allomella* Bradley, with a moderately brachypterous female, is an oreal species in the East African Ruwenzori mountains where it lives at an altitude of about 4000 m amongst the accumulated dead foliage on the trunks of *Senecio* (Compositae) (Bradley, 1965*b*: 118, figs 58, 59).

Eudarcia gallica (Petersen) (Pyrenees) with a case-making lichenivorous larva and brachypterous female (Sauter, 1985: 189, fig. 1) is probably another oreal species whilst the strong brachyptery of the female of *E. brachyptera* (Passerin d'Entréves) (Figs 3, 4; Passerin d'Entrves, 1974: 1, figs 1, 2) from Italy (Liguria) is as yet unexplained by environmental factors. The activity period of the adults, April-May, is a little earlier than that of related species but it is doubtful whether the cold season factor can be invoked. No field observations are available to decide whether the wing reduction in *E. brachyptera* could be the result of a sedentary habit similar to the situation in the Psychidae. All other *Eudarcia*, as far as known, have a similar biology but are macropterous in both sexes.

Yponomeutoidea

5. Yponomeutidae

In the Yponomeutidae wing reduction has evolved in only two unrelated genera. Strong brachyptery is known in both sexes of *Embryonopsis halticella* Eaton (Viette, 1952*a*: 3, fig.), a species inhabiting all the islands of the sub-Antarctic Kerguelen faunal province wherever its larval host-plant, the tussock grass *Poa cookii*, occurs (Crafford *et al.*, 1986: 68, figs 59–61). Slight brachyptery is observed in the females of several closely related oreal species amongst the about 20 otherwise macropterous members of the predominantly Palaearctic genus *Kessleria* Nowicki (Figs 5, 6). The wing-reduced species inhabit higher elevations of European mountain ranges (Pyrenees, Alps, Tatra mountains).

Tinearupa sorenseni Salmon & Bradley and *Campbellana attenuata* Salmon & Bradley, originally placed in the Yponomeutidae, were subsequently transferred to the Oecophoridae and Carposinidae respectively (Dugdale, 1971: 73, 134).

6. Glyphipterigidae

Moderate wing reduction appears to have evolved in the female of *Glyphipterix rugata* Meyrick on New Zealand's South Island; however, little is known about this species. Whilst the wings of the female are slightly shorter than the body, and its hind wings are distinctly narrower than those of related species, the as yet unknown male is probably macropterous. The holotype female from Tisbury (Invercargill) was beaten from the endemic *Weinmannia racemosa* Linnaeus f. (Cunoniaceae).

Gelechioidea

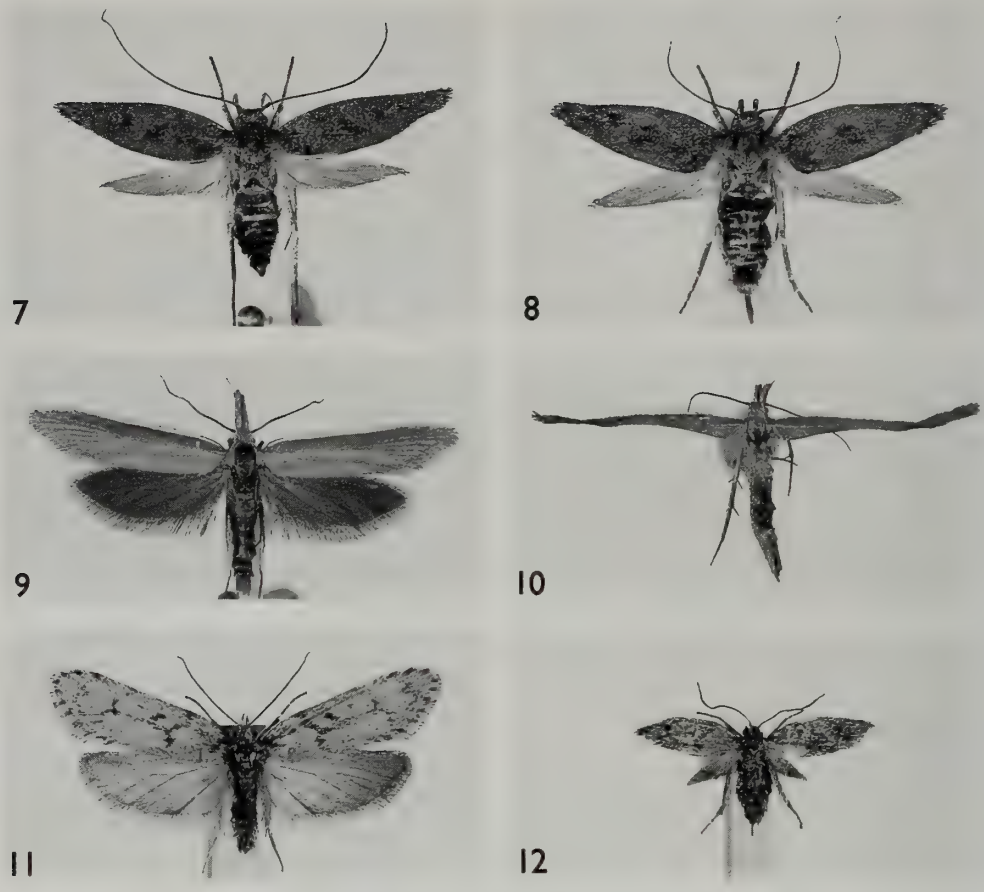
In the Gelechioidea wing reduction is found in most of the currently recognized families except the Coleophoridae (including Batrachedrinae) and the small families Agonoxenidae, Pterolonchidae, Momphidae and Holcopogonidae. All affected species are more or less strongly brachypterous, usually in the female only but occasionally in both sexes, whilst aptery is unknown. The major categories of flightlessness in response to environmental factors are represented by oceanic island species (Oecophoridae, Elachistidae, Gelechiidae), northern hemisphere cold season species (Oecophoridae) and oreal species (Blastobasidae, Symmocidae, Gelechiidae, Lecithoceridae). By far the largest number of brachypterous Gelechioidea is known from the western Palaearctic region including Madeira and the Canary Islands; some species occur in the Nearctic and Neotropical regions, on southern ocean islands, in New Zealand and Hawaii, whilst none have yet been recorded from the Afrotropical and Indo-Australian (except New Zealand) regions.

7. Oecophoridae

Ethmiinae

In the Ethmiinae wing reduction has evolved more than once independently in northern hemisphere cold season species and is restricted to the female sex. A tendency towards flightlessness is observed in the macropterous female of the Palaearctic *Ethmia pyrausta* (Pallas) the adults of which occur in May just before the birch leaves unfold (Nolcken, 1871: 671). Strong wing reduction is recorded in the female of the closely related *E. discrepitella* (Rebel) from south-eastern Russia, the adults of which are active in April to early May. Nothing is known about its biology but the male, like that of *E. pyrausta*, can be expected to fly in the sunshine.

Although in North America there are several spring-flying and autumn-flying Ethmiinae, for example *Ethmia albitogata* Walsingham (January-March), *E. plagiobothrae* Powell (March-April), *E. macelhosiella* Busck (October-November), *E. geranella* Barnes & Busck (October-November) and others, *E. charybdis* Powell, an inhabitant of the Californian San Joaquin Valley and Mojave



Figs 7–12 7, 8, *Thyrocopa apatela* (Oecophoridae: Xyloryctinae), Hawaiian Islands (Maui), (7) male, (8) female. 9, 10, *Pleurota marginella* (Oecophoridae: Oecophorinae), Austria, (9) male, (10) female. 11, 12, *Diurnea fagella* (Oecophoridae: Chimabachinae), British Isles (England), (11) male, (12) female.

Desert, is the only species with a brachypterous female (Powell, 1971, 1973).

The female of *Dasyethmia hiemalis* Danilevsky from Kazakhstan, a species with diurnal males that fly in January in the sunshine and settle on the snow, is still unknown; however, it seems safe to assume with Danilevsky (1969*a*, 1969*b*) that it will prove to be brachypterous.

Xyloryctinae

In the Xyloryctinae wing reduction is known only in the endemic Hawaiian genus *Thyrocopa* Meyrick, where it affects two or three of the about 60 species. *T. apatela* (Walsingham) (Figs 7, 8; Zimmerman, 1978: 937, figs 645, 650, 650–A), is the rare example of an oceanic island species with brachyptery in both sexes in an oreal habitat. It is endemic to East Maui, where it is a member of the aeolian ecosystem in the sparsely vegetated desert-like habitats above 3000 m on the extinct volcano Haleakala (Howarth, 1979: 14). The larva of *T. apatela* lives in loosely spun sand-clad galleries under small rocks where it feeds on trapped wind-borne organic material, predominantly the dry leaves of *Dubautia menziesii* Gray (Compositae). The brachypterous moths are unable to fly but run well and are capable of making short jumps. The habitat is exposed to strong winds and extreme temperatures. During a visit in late July 1976 there was frost on the ground at 06.00 hrs whereas the daytime temperature in the sun was high and the soil felt hot to the touch (pers. obs.). Brachyptery in both sexes suggests the influence of the wind factor; however, *Thyrocopa mediomaculata* Walsingham, which occurs in the same habitat and has an apparently identical biology, shows at best very slight wing reduction in the female and has a macropterous male which flies (pers. obs.). A related as yet undescribed oreal species on the island of Hawaii is moderately wing-reduced in

both sexes whilst the existence of other flightless forms on windswept lower slopes of the island of Molokai (Perkins, 1913: clxiv) requires confirmation.

Oecophorinae

Wing reduction in both sexes is only recorded in two Southern Ocean island species, *Borkhausenia falklandensis* Bradley in the Falkland Islands (Bradley, 1965*a*: 122, fig. 1) and *Tinearupa sorenseni* Salmon & Bradley on New Zealand's Campbell Island (Salmon & Bradley, 1956: 66, figs 10, 11) and Auckland Islands (Dugdale, 1971: 135). Wing reduction, restricted to the female sex, is known in at least four of the nine currently recognized species of the endemic New Zealand genus *Atomotricha* Meyrick (see p. 259). There is a progression of wing reduction from the macropterous female of *A. isogama* Meyrick to the strongly brachypterous *A. oeconoma* Meyrick, in which the fore wings are shorter than the abdomen and the vestigial hind wings even lack the frenulum. The adults of the brachypterous species are active in winter to early spring (August–September) and are amongst the few examples of southern hemisphere cold season species. Strong wing reduction is also observed in the female of *Chersadaula ochrogastra* Meyrick (Hudson, 1928: 272, pl. 49, fig. 4), a coastal species with grass root-feeding larvae, on New Zealand's North Island.

The strongly stenopterous female of the Central European *Pleurota marginella* (Denis & Schiffermüller) (= *P. rostrella* (Hübner)) (Figs 9, 10; Hering, 1926: pl. 5, fig. 1; Hackman, 1966: fig. 12, *P. rostrella*) is the only flightless form amongst the 70–80 species of the predominantly Palaearctic genus *Pleurota* Hübner. The fore wings are not reduced in length but are extremely narrow and have lost veins M3 and CuP whilst the hind wings are vestigial without any tubular veins although a double frenulum is still present (Baus, 1936: figs 26, 27, 28, ; 29). The larva of *P. marginella* lives in a silken tube amongst narrow-leaved grasses. The adults occur in mid-summer and the female usually hides deep in the grass; it is active in the sunshine when it can run fast and is capable of jumping in the manner of a small grasshopper (Fischer von Roeslerstamm, 1843: 295). The wing reduction in this case is clearly not the result of familiar environmental factors such as strong winds, the cold season or an oreal habitat. Instead, its evolution may have been favoured by the biology of *P. marginella* as an inhabitant of grassland, which constitutes a more or less permanent, continuous habitat in which the female does not have to resort to flight in search of oviposition sites. Elsewhere in the Gelechioidea wing reduction in summer-active grassland species is observed in the genus *Megacraspedus* Zeller (Gelechiidae) (see also p. 268).

Chimabachinae

All species of the two closely related Palaearctic genera *Diurnea* Haworth (Figs 11, 12) and *Cheimophila* Hübner are northern hemisphere cold season moths with larvae feeding on deciduous trees; the females are flightless and show various degrees of wing reduction from moderate to strong brachyptery (see for example Saito, 1979: figs 2, 4, 6). The adults of seven species are active in spring (March-May), those of one species in autumn (October-November).

8. Elachistidae

In the Elachistidae, a family of about 350 species with leaf-mining larvae in Gramineae, Cyperaceae and Juncaceae, brachyptery has evolved in both sexes of four species of the large almost world-wide genus *Elachista* Treitschke. All four affected species are inhabitants of sub-Antarctic islands (see p. 259) and there is no evidence of flightlessness or wing reduction in *Elachista* species elsewhere. The recently described *Biselachista brachypterella* Klimesch (Figs 13, 14) with moderately wing-reduced female occurs in the European Alps (Dolomites) where it was found at an altitude of about 1600 m amongst a sedge (*Carex* sp.) growing in open larch woodland. The female is flightless but is capable of jumping (Klimesch, 1990: 145, fig. 2).

9. Blastobasidae

Wing reduction was unknown in the Blastobasidae until Karsholt recently discovered at least two as yet unidentified oreal species with distinctly brachypterous females in the Peruvian Andes at an altitude of 3500 m.

10. Symmocidae

The wing reduction observed in *Ambloma brachyptera* Walsingham (Fig. 17), a species endemic to the Canary Islands (Tenerife), almost certainly affects both sexes although the female is still unknown. The moderately brachypterous male is flightless but can jump. Its habitat, the coastal sand dunes, is exposed to constant strong, storm-force north-easterly winds (Klimesch, 1985: 138, fig. 25). In contrast, the closely related *Ambloma klimeschi* Gozmány, which is also endemic to the Canary Islands (Tenerife, La Gomera) but inhabits localities more sheltered from the wind, has a macropterous male capable of flight (female still unknown) (Klimesch, 1985: 139, fig. 27). Klimesch suggested that *A. klimeschi* may be merely a macropterous morph of *brachyptera*;

Figs 13–19 13, 14, *Biselachista brachypterella* (Elachistidae), Italian Alps, (13) male, (14) female. 15, 16, *Symmoca signella* (Symmocidae), Austrian Alps, (15) male, (16) female. 17, *Ambloma brachyptera* (Symmocidae), Canary Islands (Gomera), male. 18, 19, *Megacraspedus dolosellus* (Gelechiidae), Italian Alps, (18) male, (19) female.

however, such wing dimorphism is extremely rare in the Lepidoptera and for reasons of intrasexual competition is unlikely to evolve in the male sex.

Wing reduction is also recorded in two oreal species. *Symmoca profanella* Zerny in the Haut Atlas has a strongly brachypterous female (Zerny, 1936: 142, pl. 2, figs 25, 26) whilst that of *S.*

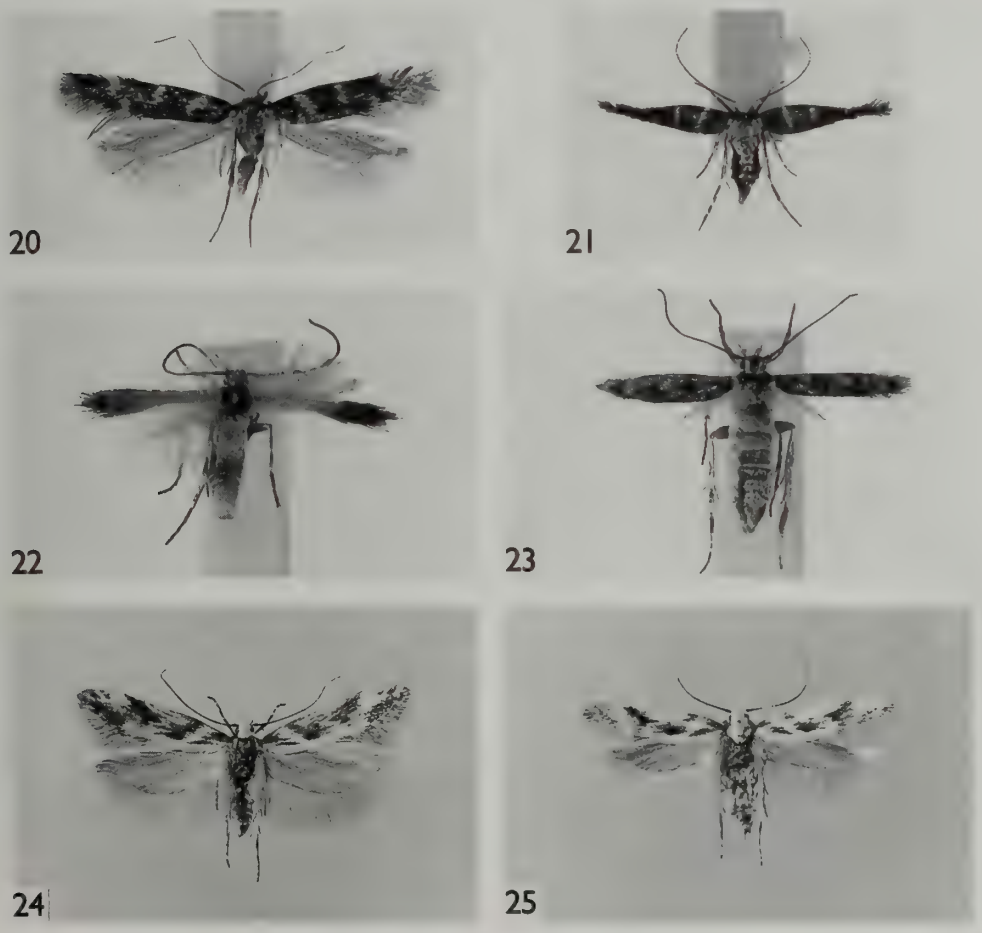
signella (Hübner) in the European Alps, although flightless (Burmann, 1947: 84), is only slightly brachypterous (Figs 15, 16).

11. Cosmopterigidae

In the Cosmopterigidae a weak tendency towards wing reduction can be observed in some European species of the genus *Vulcaniella* Riedl. *Vulcaniella pomposella* (Zeller), *V. grabowiella* (Staudinger) and *V. extremella* (Wocke) are sexually dimorphic in wing shape but only the female of the last can be classed as slightly wing-reduced (Klimesch, 1943: 65, pl. 4, figs 2, 4). The fore wing of the *extremella* female is as long as that of the male but is narrower with a conspicuous constriction near the apex. The hind wing is significantly shorter than the fore wing and its fringe is much reduced. *V. extremella* is known from southern France, eastern Austria, Yugoslavia and Hungary. Its larva is a leaf-miner in *Salvia* (Labiatae); the moth occurs in June. The extreme wing dimorphism suggests that the female is flightless; however, there are no published observations on its habits.

12. Gelechiidae

In the Gelechiidae flightlessness resulting in wing reduction, usually in the female, has evolved several times independently. Flightlessness in both sexes, with and without brachyptery, has evolved only in a few species of Gelechiinae, tribe Gnorimoschemini. Most Gelechiidae are fully winged and capable of flight but, as they are also agile runners, flying is not their only or even preferred means of locomotion. For example, the adults of many tree-inhabiting species such as *Teleiodes fugacella* (Zeller) and *T. fugitivella*



Figs 20–25 20, 21, *Eulamprotes libertinella* (Gelechiidae), Swiss Alps, (20) male, (21) female. 22, 23, *Kiwaia jeanae* (Gelechiidae) New Zealand (South Island), (22) male, (23) female. 24, 25, *Caryocolum laceratella* (Gelechiidae), Italian Alps, (24) male, (25) female.

(Zeller) on elm, *Gelechia turpella* (Denis & Schiffermüller), *G. rhombelliformis* Staudinger, *Anacampsis populella* (Clerck) and *A. innocuella* (Zeller) on poplar and aspen, and *A. blattariella* (Hübner) on birch, which usually hide in cracks of bark, often prefer to run up or around their host-tree rather than fly away when disturbed. As in many other groups of Lepidoptera, the possession of apparently well developed wings does not indicate that a particular species is a strong flier, and in many Gelechiidae the female is less inclined to fly than the male, for example *Teleiopsis albifemorella* (Hofmann) (Burmann, 1977: 142). There are even a few examples of flightlessness in both sexes of macropterous species (see below). In various species, for example *Eulamprotes wilkella* (L.), some *Chionodes* species, *Acompsia cinerella* (Clerck) and *A. tripunctella* (Denis & Schiffermüller), slight sexual differences in wing shape are observed, with the females having distally narrower fore wings than the males. Sexual wing dimorphism of such kind is seen as representing a trend towards brachyptery (Sattler, 1986: 258), and the existence of distinctly brachypterous species in *Eulamprotes* Bradley and *Acompsia* Hübner further supports this interpretation.

In most instances the brachypterous species are the only examples of wing reduction in large genera of otherwise macropterous species, for example *Eulamprotes* Bradley (1 of 10 species), *Kiwaia* Philpott (3 of 28 species), *Ephysteris* Meyrick (3 of 50+ species), *Caryocolum* Gregor & Povolný (1 of 60+ species), *Acompsia* Hübner (1 of 8 species) and *Stomopteryx* Heinemann (1 of 30+ species). In contrast, about one-third of the 30 or so *Megacraspedus* species show at least some degree of wing reduction whilst all 8 currently recognized *Sattleria* species are strongly brachypterous.

Aristoteliinae

Different degrees of wing reduction can be observed in the females of one-third of the about 30 currently recognized species of the predominantly western Palaearctic genus *Megacraspedus* Zeller (Figs 18, 19). All known species inhabit grassland, where their larvae are probably subterranean grass or grass root feeders. The adults occur in summer, and the males are usually active at dawn and dusk. Some brachypterous species inhabit high elevations, for example *M. culminicola* Le Cerf in Morocco (3200 m) and an unidentified species in Iran (2500 m), but many are found at much lower altitudes.

Daltopora felixi Povolný, an oreal species with brachypterous female (Povolný, 1979: pl. 1, fig. 33), is known only from Mongolia, where it occurs at altitudes of 1450–2500 m. The specimens were collected in the second half of June and most were attracted to light, indicating that *D. felixi* is nocturnal. The biology is unknown but the larvae can be expected to be internal feeders in one or more species of Compositae like those of the genera most closely related to *Daltopora* Povolný.

Progressive wing reduction is observed in the females of the European silver-marked species of *Eulamprotes* Bradley, but only the female of *E. libertinella* (Zeller) (Figs 20, 21), an oreal inhabitant of the European Alps, shows distinct wing reduction and could be described as stenopterous. Its fore wing is particularly narrow in the apical half, whilst the hind wing is vestigial. The females of two lowland species, *E. wilkella* (L.) and *E. superbella* (Zeller), which occur on poor sandy soils, have slightly reduced wings.

Gelechiinae (Gnorimoschemini)

Karsholt & Nielsen (1974) observed flightlessness in both sexes of the macropterous *Gnorimoschema bodillum* Karsholt & Nielsen, an inhabitant of shifting sand dunes on the North Sea coast of Denmark and northern Germany (Schleswig-Holstein). The adults, which occur in June and August, are particularly active on warm sunny days when they run fast over the ground and make jumps of about 10–25 cm. Parallel cases of flightlessness in coastal sand dune habitats are those of *Areniscythris brachypteris* Powell (Scythrididae) in California (see p. 270) and *Ambloma brachyptera* Walsingham (Symmocidae) in the Canary Islands (see p. 265); however, both sexes of these species are distinctly brachypterous. *G. bodillum* appears to be the only flightless species amongst the about 70 members of the Holarctic genus *Gnorimoschema* Busck, except perhaps for the oreal *G. elbursicum* Povolný (Iran, Elburz Mts, 3000 m) known only from a single partly damaged 'apparently brachypterous' ('offenbar brachypteren') female (Povolný, 1984: 264).

Another case of flightlessness in both sexes is that of an as yet undescribed macropterous *Scrobipalpula* species from the Falkland Islands. According to observations by C. Kirke (pers. comm.), who collected a short series of specimens (now in BMNH), the moths are flightless but jump prodigiously. The new species is closely related to Patagonian members of the predominantly New World genus *Scrobipalpula* Povolný.

In the genus *Kiwaia* Philpott, with 25 species endemic to New Zealand and three species in Nepal, wing reduction occurs in several of the New Zealand species; for example the female of *K. plemochoa* (Meyrick) is slightly wing-reduced

Figs 26–30 26, *Sattleria* species (Gelechiidae), Pyrenees. Males (left) and females (right) of *S. arcuata* (top) and *S. pyrenaica* (bottom). 27, 28, *Acompsia dimorpha* (Gelechiidae), Pyrenees, (27) male, (28) female. 29, 30, *Tegenocharis* species (Lecithoceridae), Nepal, (29) male, (30) female.

whilst that of *K. glaucoterma* (Meyrick) is strongly brachypterous. *K. jeanae* Philpott (Figs 22, 23) is one of only two species of Gelechiidae with distinct brachyptery in both sexes and at the same time the only fully brachypterous Lepidoptera species on the mainland of New Zealand. Its habitat, Birdlings Flat near Christchurch, South Island, is a windswept coastal stormbeach on the long narrow peninsula that separates Lake Ellesmere from the ocean. Moths are found from above EHWS, where they may be exposed to occasional blasts of heavy spray, to the back of the first dune-line. The ground is largely rounded shingle and sand with scattered mat-plants, mostly *Raoulia* (Compositae), where shelter is afforded by the loosely packed margins of *Raoulia* mats and interstices in the shingle (Dugdale, pers. comm.). Both sexes of *K. jeanae* are able to run very fast and make jumps of up to 15 cm (Sattler, 1988: 232).

In the Old World genus *Ephysteris* Meyrick brachyptery is known in three of the about 50 currently recognized species. *E. kasyi* Povolný was described from a single female collected at an altitude of 3000 m on the Dasht-i-Newar plateau in Afghanistan. According to an illustration of the wings that accompanies the original description (Povolný, 1968: 7, pl. 20, fig. 4) the female is moderately brachypterous; the unknown male is probably macropterous. *E. curtipennis* (Zerny), a species with macropterous male and distinctly brachypterous female, is endemic to the Haut Atlas in Morocco, where it occurs at an altitude of about 3200 m. In contrast, an as yet undescribed

species, closely related to and sometimes misidentified as *E. curtipennis*, is endemic to the Atlantic island of Madeira and is brachypterous in both sexes (Sattler, 1988: 232). A short series of this species collected in grassland at an altitude of about 1400 m (Uffen, pers. comm.), is now in BMNH.

Moderate wing reduction of the female sex is observed in only one of the more than 60 species of *Caryocolum* Gregor & Povolný. *C. laceratella* (Zeller) (Figs 24, 25), which inhabits sparsely vegetated alpine scree, is only found in the south-eastern European Alps (Julijske Alpe). The slightly brachypterous females are flightless but, like those of many other flightless oreal species, are able to run and jump (Huemer & Sattler, 1989: 256, figs 1, 2 (♂, ♀).

All known species of *Sattleria* Povolný, which inhabit the alpine zone of certain European mountain ranges, have strongly brachypterous females capable of running and jumping (Figs 26, 54, 55; Pitkin & Sattler, 1991).

Anacampsinae

Stompteryx mongolica Povolný, the only of the 30+ species of the Old World genus *Stomopteryx* Heinemann with wing reduction, is widespread and common in Mongolia, where the adults occur in June-August at altitudes of 600–2200 m. The biology is still unknown and, whilst the macropterous males are frequently attracted to light, the strongly brachypterous females are rarely observed.

The Palaearctic, predominantly European, genus *Acompsia* Hübner comprises eight species, most of which show slight sexual wing dimorphism. The female of *A. dimorpha* Petry (Figs 27, 28), an endemic of the central Pyrenees, is distinctly brachypterous, whereas other oreal species such as *A. tripunctella* (Denis & Schiffermüller) and *A. maculosella* (Herrich-Schäffer) are macropterous and apparently capable of flight in both sexes.

13. Lecithoceridae

In the Old World family Lecithoceridae wing reduction is known in the females of two unrelated genera. Brachyptery occurs in three of the seven currently recognized species of the western Palaearctic genus *Ceuthomadarus* Mann whilst the female of one species is macropterous and those of three species are still unknown (Gozmány, 1978: 52–60, pl. 1). Most species inhabit mountainous areas although only *C. funebrella* (Chrétien) and *C. naumanni* Gozmány appear to be restricted to higher altitudes (2000–2700 m). The adults of all species are summer-active but the larval habits are unknown.

An as yet unidentified *Tegenocharis* species (Figs 29, 30) with macropterous male and strongly brachypterous female was discovered in 1983 in Nepal at an altitude of about 2500 m, where the adults were collected by members of the former Lepidoptera Section (BMNH) in late May in primary montane oak forest.

14. Scythrididae

Scythrididae are inhabitants of low-growing vegetation. The adults of all species are summer-active; they are often diurnal and visit flowers. Many Scythrididae are reluctant fliers; they can run and, when disturbed, individuals sometimes jump rather than fly to safety, for example *S. inspersella* (Hübner) (Sattler, 1981: 16). As many species occur in mountainous regions at high altitudes it is surprising that none of them are brachypterous. Indeed, the only scythridid with significant wing reduction is a coastal species with strong brachyptery in both sexes. *Areniscythris brachypteris* Powell is endemic to the coastal Santa Maria sand dune system in San Luis Obispo County, California, where its larva lives in silken tunnels just beneath the surface of the sand and feeds on the partially buried green stems and leaves of a variety of plants without showing host-plant specialization. The brachypterous adults are capable of jumping 10–15 cm into the air and are then blown by the continuous strong wind over the sand like fragments of plant material. It is interesting to note that the moths produce small pits in the sand in which to shelter against the wind, a behaviour not observed in other species (Powell, 1976*b*). *A. brachypteris* is the only continental Lepidoptera species with brachyptery in both sexes; all other fully brachypterous species inhabit oceanic islands.

Tortricoidea

15. Tortricidae

In the Tortricidae wing reduction is rare but is known in several species of Tortricinae and one species of Olethreutinae (see p. 260). The only species with brachypterous male and female, *Sorensenata agilitata* Salmon & Bradley (Fig. 31), is an inhabitant of *Poa litorosa* grassland on New Zealand's sub-Antarctic Campbell Island. The adults were only observed in September–October amongst grass, where they jumped with great agility from stem to stem (Salmon & Bradley, 1956: 73, fig. 42).

The European *Exapate congelatella* (Clerck) (Figs 33, 34) and *E. duratella* (Heyden) are northern hemisphere cold season species (October-November) with strongly brachypterous females.

Figs 31–36 31, *Sorensenata agilitata* (Torticidae), New Zealand (Campbell Island), male. 32, *Pollanisus calliceros* (Zygaenidae: Procridinae), Australia (New South Wales), female. 33, 34, *Exapate congelatella* (Tortricidae), British Isles, (33) male (England), (34) female (Scotland). 35, 36, *Sphaleroptera alpicolana* (Tortricidae), Austrian Alps, (35) male, (36) female.

By contrast, *Tortricodes alternella* (Denis & Schiffermüller), a European cold season species with an adult activity period in February-March, is macropterous in both sexes and capable of flight. Flightlessness with only slight wing reduction is recorded in the heavy-bodied female of the western North American *Synnoma lynosyrana* Walsingham (Tortricinae, Sparganothini), the adults of which are active in October-November (Powell, 1976*a*). Whilst sexual dimorphism is not unusual in Sparganothini the females of most species are able to fly, except for example the macropterous female of *Synalocha gutierreziae* Powell (Powell, 1985: 65).

Although Tortricidae are well represented in the faunas of many mountain ranges in most parts of the world, only two oreal species with brachypterous females are known, *Sphaleroptera alpicolana* (Frölich) (Figs 35, 36) in the European Alps and Pyrenees and *Olethreutes orestera* Bradley in the East African Ruwenzori mountains.

A tendency towards wing reduction is also observed in the females of *Oxypteron* Staudinger, a predominantly Mediterranean genus of about 10 species, but it is unknown whether any of them are flightless. The females of several species are macropterous but those of *O. impar* Staudinger

(southeastern Europe, Turkey) and *O. exiguana* (de la Harpe) (Sicily, North Africa) are slightly brachypterous. Whilst some *Oxypteron* are cold season species, for example *O. homsana* (Amsel) (Syria, Jordan: November–December; female unknown, possibly brachypterous) and perhaps *O. impar* (September–October), that cannot be said for *O. exiguana* (August–September).

Zygaenoidea

16. Heterogynidae

The systematic status of the small family Heterogynidae, which comprises two genera with an uncertain number of species, is not yet clear and its current placement in the Zygaenoidea is tentative. The females of the Mediterranean genus *Heterogynis* Rambur are apterous (Freina & Witt, 1990: pl. 10) and have strongly reduced mouthparts and legs. According to observations on *H. penella* (Hübner) (Daniel & Dierl, 1966) the female stays on the cocoon after emergence from the pupa, because its head and legs remain firmly attached to the pupal skin. After mating, the female returns into the cocoon and re-enters the pupal exuviae where it lays its eggs. As in the Psychidae, the loss of wings and reduction of legs in the female can be interpreted as the direct result of sedentary habit. The females of the South African genus *Janseola* Hopp are unknown.

17. Zygaenidae

The only example of wing reduction in the Zygaenidae, a family of about 1000–1500 species worldwide, is the micropterous female of the Australian *Pollanisus calliceros* Turner (Procridinae) (Fig. 32), a species recorded from mountaineous areas of about 600–1500m in New South Wales and Tasmania. Only a single female is known to date and was described as having simple antennae, a broad abdomen with grey anal tuft, small but normal thorax and legs and very small rudimentary wings (Turner, 1926: 443–444); no information on its habits is available. As far as known the females of all other *Pollanisus* species are macropterous and can fly.

18. Somabrachyidae

The systematic status and placement of the small family Somabrachyidae in the Zygaenoidea are also uncertain. *Somabrachys* Kirby, the only included genus, is of Mediterranean distribution (North Africa – Syria) and comprises between 1 and 20 species depending on author (Freina & Witt, 1990: 48–50, pl. 6, figs 54–91). The apterous females superficially resemble those of *Orgyia antiqua* (L.) (Lymantriidae) but, in contrast to the latter, have well developed legs and are able to run fast (Seitz, 1912: 336, pl. 50 d). The macropterous males are nocturnal and are attracted to light. With an adult activity period in September – November all known *Somabrachys* are cold season species.

Copromorphoidea

19. Carposinidae

The small family Carposinidae is mostly tropical with the majority of its about 200 species occurring in the Indo-Australian region. Wing reduction is known only in *Campbellana attenuata* Salmon & Bradley, an inhabitant of New Zealand's sub-Antarctic Campbell Island with strong brachyptery in both sexes (Salmon & Bradley, 1956: 68, fig. 38). The biology is unknown but the adults live amongst the tussock and are able to jump like small grasshoppers. *C. attenuata* was originally described in the Yponomeutidae but was subsequently transferred to the Carposinidae (Dugdale, 1971: 73).

Pyraloidea

20. Pyralidae

In the Pyralidae, with an estimated 25,000 species possibly the largest Lepidoptera family, examples of wing reduction are known in the subfamilies Pyralinae, Crambinae, Acentropinae, Pyraustinae and Scopariinae. There are two oceanic island species (Scopariinae, Pyraustinae) with brachyptery in both sexes, several oreal species (Crambinae, Pyraustinae) with more or less brachypterous females and an aquatic species (Acentropinae) with wing dimorphism in the female (a macropterous and a brachypterous form). However, there are apparently no wing-reduced cold season Pyralidae.

Pyralinae

Wing reduction is known in several of the dozen species of the Palaearctic genus *Synaphe* Hübner. The females of some species, for example *S. punctalis* (Fabricius), *S. amuralis* (Hampson), *S. bombycalis* (Denis & Schiffermüller) (Figs 37, 38) and *S. moldavica* (Esper), have narrower wings and proportionately longer abdomens than the males, but extreme brachyptery is only developed in *S. oculatalis* (Ragonot) from Northwest Africa (Zerny, 1936: 121, pl.2, fig. 12 (♀)). The reasons for this trend towards brachyptery in *Synaphe* are still unclear, because the females are not noticeably heavy-bodied and none of the species is restricted to the cold season or confined to oreal habitats. The adults of *S. oculatalis* occur in late August – early October, too early to qualify

Figs 37–42 37, 38, *Synaphe bombycalis provincialis* (Pyralidae: Pyralinae), Spain, (37) male, (38) female. 39, *Udea hageni* (Pyralidae: Pyraustinae), Tristan da Cunha, male. 40, *Exsilirarcha graminea* (Pyralidae: Scopariinae), New Zealand (Campbell Island) male. 41, 42, *Apleria* sp. (Geometridae: Larentiinae), Chile (Magallanes), (41) male, (42) female.

clearly as cold season species, and inhabit lowland localities, although they reach altitudes of about 2000 m in the Moyen Atlas.

Crambinae

A tendency towards sexual dimorphism of the wing shape is noticed in several Palaearctic Crambinae, in which the females sometimes have slightly narrower, more pointed fore wings than the males but are still capable of flight, for example *Agriphila poliella* (Treitschke) (Bleszynski, 1965: pl. 14, figs 161–1 (♂), 161–2 (♀)). Stronger wing reduction coupled with flightlessness is recorded in the southern European oreal *Catoptria digitella* (Herrich-Schäffer) (Bleszynski, 1965: pl. 18, figs 215–1 (♂), 215–2 (♀)), *C. biformella* (Rebel) (Bleszynski, 1965: pl. 20, figs 234–1 (♂), 234–2 (♀)) and *C. majorella* (Drenowski) (Bleszynski, 1965: pl. 20, figs 235–1 (♂), 235–2 (♀)). Slight wing reduction is also noted in the female of *Fernandocrambus falklandicellus* (Hampson) in the Falkland Islands, but field observations have shown that it is still capable of flight (Kirke, pers. comm.).

Amongst the New Zealand Crambinae a tendency towards wing reduction is observed in several of the about 50 species of the endemic genus *Orocrambus* Purdie. For example, the female of *O. lectus* (Philpott), an inhabitant of subalpine to alpine regions on South Island, is distinguished from the male by an acutely pointed fore wing and slightly reduced hind wing (Hudson,

1939: pl. 56, fig. 17 (♀); Gaskin, 1975: fig. 53 (♂)) and may be flightless. According to Gaskin (1975: 308), the unknown female of *O. crenaeus* (Meyrick), a species of alpine grassland on South Island, may be brachypterous; however, strong wing reduction is only observed in the indisputably flightless female of *O. lindsayi* Gaskin, an endemic of Mount Ida on South Island. Whilst the as yet unknown male of *lindsayi* is almost certainly macropterous, the female has narrow, lanceolate fore wings and similarly shaped but much shorter hind wings (Gaskin, 1975: figs 22d, 55). Although currently retained in a separate genus, *Kupea electilis* Philpott probably is merely another *Orocrambus* species with some degree of wing reduction. The loss of vein M2 in both fore and hind wing of the male may be interpreted as a first step towards wing reduction whilst the unknown female is suspected of being brachypterous (Gaskin, 1975: 345, figs 22f, 82). Flightlessness and associated wing reduction would not surprise in *K. electilis* because it shares its stormy coastal habitat Birdlings Flat with at least one other Lepidoptera species that is strongly brachypterous in both sexes (*Kiwaia jeanae* Philpott, Gelechiidae, see p. 269).

Acentropinae

Acentria ephemerella (Denis & Schiffermüller) (= *Acentropus niveus* (Olivier)), distributed in the western Palaearctic and Nearctic regions, is the only known aquatic moth with brachyptery. Whilst the male is always fully winged and capable of flight, in the dimorphic female a macropterous and a brachypterous form are known. The larva of *A. ephemerella* lives submerged on various water plants and, whilst the macropterous males and females leave the water, the brachypterous females remain permanently under water, where they crawl about plants or swim with the aid of their meso- and metathoracic legs which are equipped with a fringe of long hairs. The adults are nocturnal – the macropterous males and females are attracted to light – and the brachypterous female swims to the surface where is raises the apex of its abdomen out of the water to attract males, one of which eventually lands on the female's back and effects the copula. Brachyptery in this case is undoubtedly an adaptation to life under water, where fully developed wings would be disadvantageous. However, the mechanism for the female wing dimorphism is not yet fully understood. The suggestion that a brachypterous generation may alternate with a macropterous one was not confirmed by the observations of Berg (1941), who believed that environmental factors such as higher water temperatures in summer were responsible for the development or macropterous females.

Pyraustinae

Slight wing reduction in the female is recorded for *Nomophila heterospila* (Meyrick), a species found in the South American Andes at an altitude of about 3000–5000 m (Munroe, 1973: 199, figs 39, 41 (♂), 40, 42 (♀). It is not known whether the reduction is an indication of flightlessness; however, a comparison with analogous cases of sexual wing dimorphism in some other Lepidoptera, for example certain Gelechiidae, suggests that the female of *N. heterospila* is still capable of flight. Some wing reduction is also recorded in *Udea hageni* Viette (Fig. 39) on Tristan da Cunha in the South Atlantic. The males are flightless and stay on the ground (Viette, 1952*b*: 3, 18); the unknown female is almost certainly brachypterous.

Scopariinae

Both sexes of *Exsilirarcha graminea* Salmon & Bradley, an inhabitant of New Zealand's sub-Antarctic Campbell Island and Auckland Islands, are strongly reduced (Fig. 40). The adults were observed in September in large numbers amongst the tussock grass *Poa litorosa*; they walk and are capable of jumping (Salmon & Bradley, 1956: 73–77, figs 24–30). Female brachyptery is known in *Protyparcha scaphodes* Meyrick, on the Auckland Islands. Both species were previously considered to be Crambinae but are now included in the Scopariinae (Dugdale, 1988: 159).

Geometroidea

21. Geometridae

With about 20,000 species the Geometridae are one of the largest Lepidoptera families and, at the same time, also the family with by far the largest number of species with wing reduction (disregarding the Psychidae). Within the Geometridae brachyptery has evolved many times independently and is recorded in the subfamilies Oenochrominae, Larentiinae (tribes Xanthorhoini and Operophterini) and Ennominae (tribes Semiothisini, Bistonini and Gnophini). Although in this family flightlessness and wing reduction are usually restricted to the female sex, there appears to be a slight tendency towards reduction in the males of some species endemic to New Zealand's sub-Antarctic islands. For example in *Asaphodes oxyptera* (Hudson) and *A. campbellensis* (Dugdale) (Larentiinae), both species with brachypterous females, the wings of the males are distinctly narrower than those of related *Asaphodes* species in mainland New Zealand. Reduction in the size

of the hind wings, as it is observed in the males of many Larentiinae with normal macropterous females, for example *Tatosoma* Butler, *Tympanota* Warren and *Sauris* Guenée (Dugdale, 1980), is disregarded here because it does not impair the ability to fly and is unrelated to the phenomenon of flightlessness. In the Geometridae all stages of wing reduction, from weak brachyptery to microptery and aptery, have been observed. For example in the alpine *Elophos zelleraria* (Freyer) or the arcto-alpine *Pygmaena fusca* (Thunberg) wing reduction is usually slight and females may still be able to fly at least short distances, whilst flight is almost certainly impossible for the females of Japanese cold season *Protalcis* species with wings only about half the size of those of the males (Inoue, 1982: pl. 98, figs 12–15). Greater reduction can be seen in the females of *Alsophila* Hübner, *Operophtera* Hübner (Fig. 56), *Lerannis* Wehrli and others, in which the wings are usually shorter than the body. Various species referred to as apterous in the literature, for example *Erannis* species (Fig. 57) and *Chondrosoma fiduciarium* Anker (Fig. 43), are in fact micropterous and still possess wing vestiges although these are often concealed in the dense thoracic hair cover where they can only be found with careful examination. True aptery is rare but is confirmed for *Cheimoptena pennigera* Danilevsky (Danilevsky, 1969*a*: 183, fig. 10). A rare example of stenoptery is the female of the central Asiatic *Spartopteryx kindermannaria* (Staudinger) (Figs 44, 45; Wehrli, 1941: 466, pl. 41 b).

As far as known, in the Geometridae all wing-reduced females have fully developed legs and are motile; however, whilst they are able to walk, they

Figs 43–47 43, *Chondrosoma fiduciarium* (Geometridae: Ennominae), Austria; male (left), female (right). 44, 45, *Spartopteryx kindermannaria* (Geometridae: Ennominae), Siberia, (44) male, (45) female. 46, 47, *Elophos caelibaria* (Geometridae: Ennominae), Austrian Alps, (46) male, (47) female.

do not usually run fast and appear to be unable to jump. Most of the Geometridae with wing-reduced females are northern hemisphere cold season species, for example *Alsophila* Hübner, *Alsophiloides* Inoue, *Inurois* Butler (Oenochrominae), *Operophtera* Hübner (Larentiinae), *Apocheima* Hübner, *Lycia* Hübner, *Cheimoptena* Danilevsky, *Chondrosoma* Anker, *Agriopis* Hübner, *Erannis* Hübner, *Pachyligia* Butler, *Descoreba* Butler and others (Ennominae). A southern hemisphere cold season species with strongly brachypterous female is *Zermizinga indocilisaria* Walker (Ennominae) in New Zealand. Some cold season species are diurnal, for example *Lycia zonaria* (Denis & Schiffermüller), *Cheimoptena pennigera* Danilevsky and *Chondrosoma fiduciarium* Anker, and their males usually fly under sunny conditions when they are able to absorb solar radiation to raise their thoracic temperature high enough to allow the flight musculature to operate (see p. 253). However, most species are nocturnal and their males are adapted to flying at low thoracic temperatures (see p. 253).

The large number of brachypterous cold season species, which represent at least three independent evolutionary lineages within the Geometridae, indicates the potential in that family to respond with wing reduction to appropriate environmental conditions. It is therefore surprising that the incidence of brachyptery is rather low amongst oreal species although the Geometridae are extremely well represented in the highland faunas of the world. In the Palaearctic region a more or less pronounced trend towards flightlessness is observed in the females of alpine Ennominae, particularly in the tribe Gnophini, but a significant degree of wing reduction has only evolved in several of the about 10 species of the genus *Elophos* Boisduval. Whilst the female of *E. zelleraria* (Freyer) is distinctly smaller than the male, but can still be described as macropterous, those of most other species are more strongly brachypterous, for example *E. caelibaria* (Herrich-Schäffer) (Figs 46, 47) and *E. zirbitzensis* (Pieszczek) in the European Alps (Forster & Wohlfahrt, 1980: pl. 24, figs 40–43; pl. 25, figs 1–8) as well as *E. iveni* (Erschoff) (Wehrli, 1953: 621) and *E. banghaasi* (Wehrli) (Wehrli, 1922: 27, pl. 2, figs 41, 56) in Central Asia.

In the European oreotundral *Pygmaena fusca* (Thunberg) the female has noticeably narrower wings than the male (Forster & Wohlfahrt, 1980, pl. 25, figs 44 (♂), 52 (♀)) and their length, according to Hackman (1966: 2), varies considerably; however, whilst many authors considered the female as flightless or nearly so, Wehrli (1953: 640) disputed this and described it as a skilful flier. Slight wing reduction is also found in the female of *Sciadia tenebraria* (Esper) in the European mountains (Pyrenees, Alps, Appenin), but no observations on its ability to fly are available.

In East Africa several *Xanthorhoe* species (Larentiinae) with strongly brachypterous females, e.g. the nocturnal *X. alluaudi* (Prout) and the diurnal *X. barnsi* (Prout) and X. *wellsi* (Prout), inhabit the ericaceous zone and alpine zone of the Ruwenzori mountains (Fletcher, 1958: 77, figs 12–18).

In New Zealand wing reduction in oreal species is found in an unidentified species of Oenochrominae (McQuillan, 1986: 263) and in the large genus *Asaphodes* Meyrick (Larentiinae). For example the female of *A. nephelias* (Meyrick) differs from the male by narrower, more pointed fore wings but is still able to fly (Dugdale, pers. comm.) whilst the brachypterous female of *A. dionysias* (Meyrick) is flightless. Moderate wing reduction is observed in the female of *Aponotoreas villosa* (Philpott) (Hudson, 1928: 123, pl, 15, figs 23 (♂), 24 (♀)).

In South America, the subcontinent most poorly explored for wing-reduced forms, an as yet undescribed species of *Apleria* Warren (Larentiinae) (Figs 41, 42) with strongly brachypterous female was discovered in southern Chile, Munoz Gomero Peninsula (Magallanes). According to Perry (pers. comm.) it occurs at an altitude of about 500 m in low vegetation near and above the treeline of *Nothofagus antarctica* forest, where a series of males and females, now preserved in BMNH, was collected in the daytime in March 1973; some adults were also observed above the treeline at about 1300 m.

A case of strong female brachyptery unexplained by seasonal factors or the biotope is that of the Holarctic *Itame loricaria* (Eversmann) (Ennominae, Semiothisini), a summer-active moth with birch-feeding larva. As far as known, no other *Itame* species is wing-reduced or flightless.

Bombycoidea

22. Lasiocampidae

The family Lasiocampidae, with representation on all continents, comprises about 1000 species the adults of which are usually short-lived and, with reduced mouthparts, non-feeding. Although they are mostly heavy-bodied and the sluggish females fly little, particularly whilst still carrying their full egg complement, wing reduction is rare in this family and is only recorded in two genera in the western Palaearctic region and one monotypic genus in southern Africa. In each case the reduction is confined to the female sex and there are no

examples of wing reduction or diminished ability to fly in the male. The females of all affected species have vestigial wings and thus must be classed as micropterous, although they were sometimes incorrectly referred to as wingless; no example of a lesser degree of wing reduction is known. Reduction of the wings in Lasiocampidae is probably a consequence of the more or less sedentary habit of the gravid female with its heavy abdomen.

As in the Palaearctic region the adult activity periods of many Lasiocampidae extend into the autumn and sometimes winter, it could be argued that wing reduction is a response to adult life in the cold season. However, the adult activity of such species usually commences in summer (July or August) so that only part of the population would be exposed to autumn or winter conditions. By contrast, true winter species such as *Trichiura ilicis* (Rambur) (Iberian Peninsula, North Africa; December-April) and *Stoermeria regraguii* (Lucas) (Morocco; December-January) have macropterous females. Moreover, all known micropterous species are confined to southern Europe and North Africa, whilst the cold season Lasiocampidae occurring in the harsher climate of central and northern Europe are without exception macropterous, for example *Trichiura* Stephens, *Poecilocampa* Stephens and *Eriogaster* Germar.

Micropteryy in the female is observed in all taxa of the Mediterranean genus *Chondrostega* Lederer (Freina & Witt, 1987: 330, pl. 25, figs 1–11); however, the total number of species, which is still unknown because the taxonomic status of most of the currently recognized 15 species is uncertain, may not exceed three or four. The North African *Lasiocampa staudingeri* Baker (Freina & Witt, 1987: 362, pl. 28, figs 39–41) which has an adult activity period in August-January, is the only *Lasiocampa* species with wing reduction. Related species with similarly late flight periods, for example *L. serrula* (Guenée) (southern Spain, North Africa; September-November) and *L. eversmanni* (Eversmann) (southern Russia; August-October), have macropterous females (Freina & Witt, 1987: 359, 360, pl. 29, figs 6–15).

The only non-Palaearctic lasiocampid with wing-reduced female, *Mesocelis montana* (Stoll) (Pinhey, 1975: 119, pl. 22, figs 500a (♂), 500b (♀), is found in southern Africa, where the adults are active in summer (November). With a small head, very small eyes, much reduced antennae, mouthparts and legs, and vestigial wings, the heavy-bodied female resembles those of some Lymantriidae. After emerging from the pupa the female remains within the cocoon, where it lays about 30–100 eggs. During oviposition the dense cover of body hair is rubbed off and fills the cocoon as loose fluff which may have irritating properties and acts to protect the eggs from predators (Hesse, 1935). Although both sexes normally occur, Taylor (1950, 1954) observed a parthenogenetic population, a sample of which he reared in captivity for at least eight generations. The moths reproduced vigorously and produced all-female offspring.

Noctuoidea

23. Lymantriidae

The family Lymantriidae has an almost worldwide distribution and comprises about 2500 species. Their usually summer-active adults are non-feeding – those of most species have reduced mouthparts – and many species are apparently protected from predators by distasteful substances in conjunction with aposematic coloration. The larvae are mostly foliage feeders on a wide variety of broad-leaved and coniferous trees and shrubs; many species are polyphagous whilst others are more restricted in their diet although few are monophagous.

In many species the females are heavy-bodied; they are reluctant fliers and some are practically flightless although still in possession of fully developed wings, for example the Arctic *Gynaephora rossii* (Curtis) and *G. groenlandica* (Wocke) or *Lymantria dispar* (L.) (Ferguson, 1978: 20, 21, 94). Wing reduction, restricted to the female sex, has evolved in several independent lineages and can be interpreted as a consequence of the females' reduced motility and sedentary habit. In most cases the wing-reduced females are micropterous or even apterous, with small thorax, more or less reduced legs and a large egg-filled abdomen; however, brachyptery is also known. After emerging from the pupa micropterous and apterous females usually stay on the pupal cocoon onto which they lay their eggs after mating with the frequently diurnal males.

The genus *Orgyia* Ochsenheimer (including *Teia* Walker and *Hemerocampa* Dyar, which are sometimes treated as separate genera) occurs on all continents and comprises about 45 species. Whilst a few of them have macropterous females, e.g. the African *O. basalis* (Walker) (Pinhey, 1975: 179, pl. 47, figs 863 a-c), or are brachypterous, e.g. the African *O. hopkinsi* Collenette, most Palaearctic, African, Indo-Australian and American species are micropterous, e.g. *O. antiqua* (L.) (Fig. 60), and some even apterous, e.g. *O. dubia* (Tauscher) (Kozhanchikov, 1950: fig. 2) and *O. ericae* (Germar) (Heitmann, 1934: 180). For further examples of wing reduction in *Orgyia* see

Ferguson (1978: pls. 7, 8) and Freina & Witt (1987: pl. 15). A rare case of wing dimorphism is recorded in the Japanese *O. thyellina* Butler; the females of the first generation are macropterous (Inoue, 1982: pl. 148, figs 9 (♂), 10 (♀)), those of the second generation to about one-third macropterous and two-thirds strongly brachypterous or micropterous and the third generation almost totally micropterous (Cretschmar, 1928: 298). Hackman (1966: 4, fig. 2), misinterpreting an illustration depicting a female with partly removed wings (Kozhanchikov, 1950: fig. 1), erroneously recorded *Gynaephora lugens* Kozhanchikov (junior synonym of *G. rossii* (Curtis)) as brachypterous.

Moderate brachyptery, without loss of wing veins, is observed in the female of *Penthophera* morio (L.) (Eggers & Gohrbandt, 1938: 267, fig. 2; Freina & Witt, 1987: 206, pl. 15, figs 3–6), an inhabitant of open places in south-eastern Europe, where its larva feeds on a variety of grasses.

Brachyptery and micropteryhave evolved in the females of several Indo-Australian species of *Lymantria* Hübner, an Old World genus of about 150 species, the adults of which frequently are aposematically coloured. The females of some species are flightless but nevertheless macropterous, and retention of the non-functional wings may in this case be advantageous because it enhances the effect of the aposematic coloration. In contrast, those of several Indo-Australian species are brachypterous, for example *L. obfuscata* Walker and *L. turneri* Swinhoe, whilst others such as *L. detersa* Walker, *L. incerta* Walker and *L. ampla* (Walker) are micropterous.

As far as known the females of all eight species of *Bracharoa* Hampson, a genus restricted to sub-Saharan Africa, are strongly wing-reduced, probably apterous. The female of *B. dregei* (Herrich-Schäffer) 'apparently deposits her eggs within the cocoon' (Taylor, 1949: 84, pl. 1, figs 18, 18A (♂, ♀)); however, it is not clear from this statement whether the female remains inside the cocoon after emerging from the pupa or sits on the outside and merely lays its eggs into it.

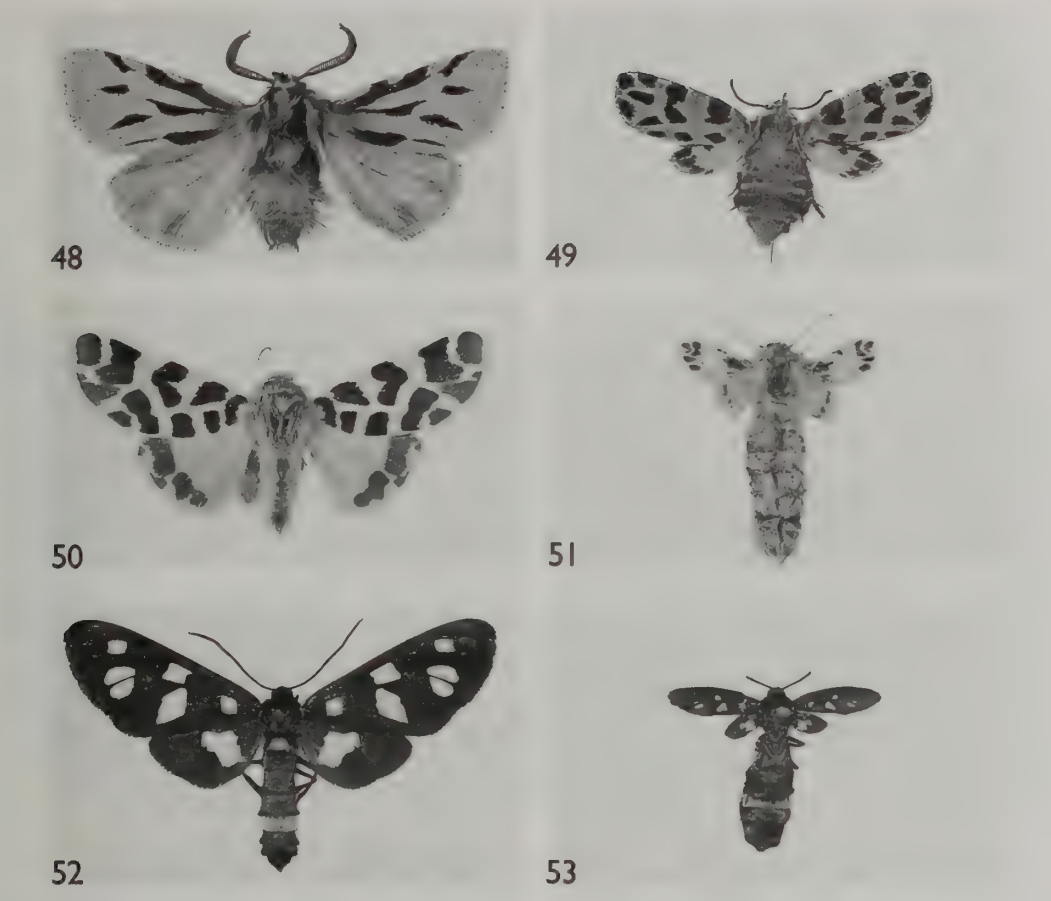
Further examples of wing reduction are the African *Aroa melanoleuca* Hampson (♀ micropterous or apterous) (Pinhey, 1975: 176, pl. 44, figs 841a (♂), 841 b (♀)), Asiatic *Lachana ladakensis* Moore (♀ micropterous or apterous), *Laelia heterogyna* Hampson (♀ brachypterous), *Dasorgyia pumila* Staudinger (♀ slightly brachypterous) and *D. selenophora* Staudinger (♀ micropterous or apterous) and the Australian *Iropoca rotundata* (Walker) (♀ micropterous) (Common, 1990: 428, figs 43.5, 43.6). The apterous females of an as yet unidentified species (male still unknown) probably belonging to the Lymantriidae were discovered in May and October 1989 at an altitude of 3000 m in the South African Drakensberge sitting in the sun (Scholtz in litt.).

24. Arctiidae

The family Arctiidae, here taken to include the Ctenuchinae and Thyretinae which are sometimes considered separate families, is distributed on all continents and comprises about 10,000 species. The mostly summer-active adults are often aposematic; they are usually non-feeding, with reduced mouthparts, and many species are heavy-bodied. In the females there is a widespread tendency towards flightlessness, and various degrees of brachyptery and micropteryhave evolved in several independent lineages. Strong reduction of the hind wings is observed in the males of certain South American Ctenuchinae but does not impair their ability to fly; in the most extreme case, *Diptilon culex* Draudt (Draudt, 1915: 120, pl. 19 e), the hind wings of the male are reduced to tiny appendages which are hidden in the thoracic scale cover. The larvae of many Arctiidae are polyphagous, mostly on herbaceous plants.

Wing reduction in the females of Arctiidae may generally be interpreted as a consequence of their low motility and sedentary habit, although in several cold season *Ocnogyna* species and a few oreal species some response to environmental factors may additionally be involved.

In the Lithosiinae a high degree of flightlessness is recorded in the females of the European genus *Setina* Schrank (= *Endrosa* Hübner); however, wing reduction is at best slight (Freina & Witt, 1987: pls 3, 4). According to observations on this genus by Burmann (1957) in the European Alps, both sexes emerge from the pupae in the early hours of the morning, usually before 10.00 hrs. The diurnal males, which fly in the sunshine, commence their courtship flight soon after sunrise and mate with the freshly emerged females, which at that time still sit on or near their pupal cocoons. Mating sometimes takes place before the female has fully expanded its wings. Egg-laying begins soon after the copula has separated, and the first batch of eggs is often deposited not far from the pupal site. After having laid most of its eggs the female may fly short distances, usually in late afternoon, thus ensuring some dispersal of its egg complement. Strong wing reduction is known in *Xanthodule* Butler, an endemic Australian genus with two species. After emerging from the pupa the female stays on the outside of its cocoon where it mates and deposits its eggs in the manner of *Orgyia* species (Common, 1990: 437, pl. 31.4). According to McQuillan (1986: 271) the female of the Tasmanian *Thermeola tasmanica* Hampson is



Figs 48–53 48, 49, *Ocnogyna parasita* (Arctiidae: Arctiinae), Hungary, (48) male, (49) female. 50, 51, *Cymbalophora haroldi* (Arctiidae: Arctiinae), Algeria, (50) male, (51) female. 52, 53, *Syntomis mestralii* (Arctiidae: Ctenuchinae), (52) male (Lebanon), (53) female (Israel).

also flightless; however, it is not stated whether it has reduced wings.

The largest number of wing-reduced Arctiidae is found in the subfamily Arctiinae, particularly amongst north-west African species. In the western Palaearctic genus *Coscinia* Schrank appreciable wing reduction is known in the North African *C. libyssa* (Püngeler), which at the same time shows some variation in the degree of brachyptery, with the female of the oreal subspecies *C. libyssa liouvillei* Le Cerf in the Atlas mountains being more strongly reduced than that of the nominate subspecies at low elevations (Freina & Witt, 1987: 112, pl. 5, figs 44–49). Varying degrees of wing reduction affect all females of the about 10 predominantly south-western Palaearctic cold season species of the genus *Ocnogyna* Lederer, from moderate reduction in some forms of *O. zoraida* (Graslin) through distinct brachyptery in *O. parasita* (Hübner) (Figs 48, 49) to microptery in *O. baetica* (Rambur) and possibly aptery in *O. pudens* (Lucas) (Freina & Witt, 1987: pl. 5, figs 50–66, pl. 6, figs 1–28; Seitz, 1910: 76, pl. 14; Draudt, 1931*b*: 72, pl. 6). Strong brachyptery is also known in the female of *Tancrea pardalina* Püngeler from Turkestan (Püngeler, 1899: 95, pl.8, figs 1a (♂), 1b (♀); Seitz, 1910: 75, pl. 14 b (♂), 16 a (♀)). There must be some doubt that an Algerian specimen, now preserved in BMNH, with narrow fore wings and short, curiously curved hind wings represents the normal female of *Maurica breveti powelli* (Oberthür) (Oberthür, 1911: pl. 78, fig. 711; Freina & Witt, 1987: pl. 6, fig. 40) because the female of the nominate subspecies *M. breveti breveti* (Oberthür) is macropterous.

Whilst the females of the North African *Cymbalophora haroldi* (Oberthür) (Figs 50, 51; Freina & Witt, 1987: pl. 8, figs 9–13) and Mediterranean *C. rivularis* (Ménétriés) (Freina & Witt, 1987: pl. 8, figs 1–6) are respectively brachypterous and

micropterous, those of other *Cymbalophora* species are macropterous. Moderate brachyptery is observed in the female of *Spilosoma bretaudiaui* (Oberthür) from Tibet and Nepal (Seitz, 1910: 97, pl. 17 h (♂, ♀)) whilst those of all other species in that genus are macropterous. Outside the Palaearctic region microptery is observed in the females of three species of *Metacrias* Meyrick, a genus endemic to New Zealand. *M. erichrysa* Meyrick and *M. huttoni* (Butler) are restricted to alpine habitats but *M. strategica* Hudson appears to be more widespread. The males are diurnal and the females remain within their cocoons for mating and ovipositing (Gibbs, 1962: 153). Female microptery and a similar biology are also known in the closely related Australian genus *Phaos* Walker, which has oreal species in the Australian Alps and Tasmania (McQuillan, 1986: 270).

In South America strong wing reduction occurs in several of the about 75 species of *Paracles* Walker; for example the densely hairy females of the Argentinian *P. deserticola* Berg (Seitz, 1920: 321, pl. 41 d (♂, ♀)), *P. brittoni* Rothschild and *P. insipida* Rothschild are micropterous, that of the Chilean *P. rudis* Butler strongly brachypterous. Another species with micropterous female, the oreal *P. imitatrix* Rothschild in the Peruvian Andes (about 5000 m), may not be congeneric with the preceding ones.

In the Ctenuchinae some wing reduction can be observed in the females of the large Old World genus *Syntomis* Ochsenheimer. *Syntomis* species are summer-active, diurnal, aposematic moths with often sluggish females. Brachyptery is recorded in the middle-eastern *S. mestralii* Bugnion (Figs 52, 53; Seitz, 1910: 38, pl. 9 b (♂), 9 d (♀)), *S. antiochena* Lederer (Seitz, 1910: 38, pl. 9 d (♂, ♀)) and *S. libanotica* Bang-Haas (Draudt, 1931*a*: 57, pl. 5 e (♂, ♀)). Outside the Palaearctic region brachyptery occurs in the female of the South African *Epitoxis amazoula* Boisduval. Wing reduction is also known in the South American genus *Eurota* Walker, where the female of the Argentinian *E. spegazzinii* Jörgensen is strongly brachypterous (Draudt, 1915: 98, pl. 16 c (♂), pl. 26 , (♀), and is recorded in the female of the closely related *E. strigiventris* Guerin from Brazil, Argentina and Bolivia (Draudt, 1915: 98).

In the small subfamily Thyretinae, strong brachyptery in the female of the South African *Automolis meteus* (Stoll) (Pinhey, 1975: 144, pl. 36, figs 647a, 647b) is the only known case of wing reduction. Other species have macropterous females.

25. Noctuidae

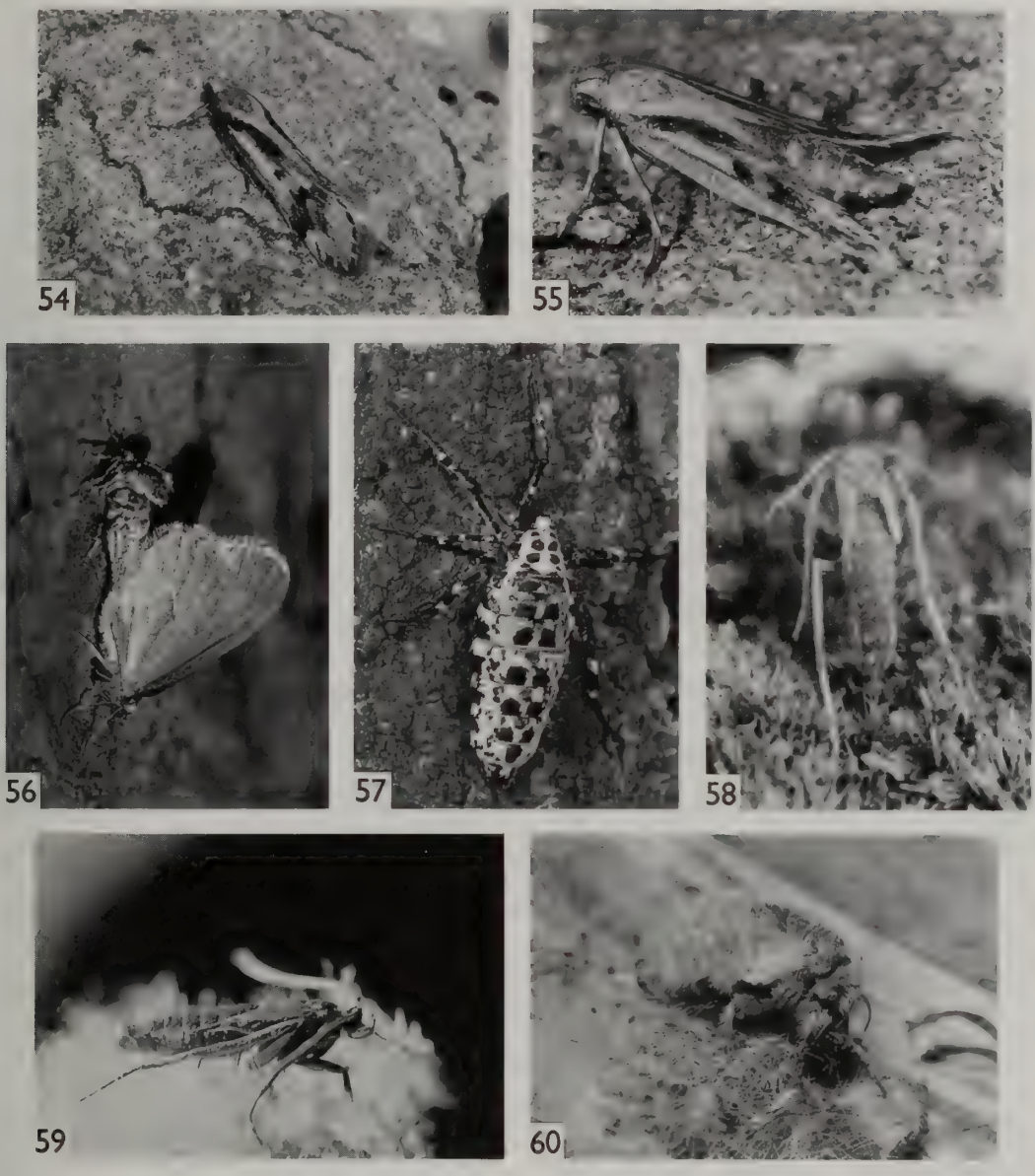
With about 20,000 species the cosmopolitan Noctuidae are one of the largest Lepidoptera families. As adults, Noctuidae are relatively long-lived, mostly nocturnal moths with well developed mouthparts; the majority of species feeds on a wide variety of liquid plant substances such as nectar, sap from injured trees, decaying fruit etc. Although many species are relatively heavy-bodied, most of them are enduring fliers with rapid wing beat and excellent manoeuvrability.

Wing reduction has evolved independently in several lineages, and examples are known in the subfamilies Acronictinae, Cuculliinae and Hadeninae but mostly in the Noctuinae. Whilst in the noctuoid families Lymantriidae and Arctiidae wing reduction is confined to the female sex of the affected species and is primarily, if not exclusively, the consequence of sedentary habit, in the Noctuidae it is a response to environmental factors and in some instances affects both sexes. In contrast to the Lymantriidae and Arctiidae the wing-reduced Noctuidae are motile and able to run fast, for example *Agrotis fatidica* (Hübner) (Vorbrodt, 1928: 54; Bergmann, 1931: 30), but there is no indication that any of them are capable of jumping.

Wing reduction in both sexes or only in the female is recorded in several species on southern ocean islands. On the South Atlantic island of Tristan da Cunha *Dimorphinoctua pilifera* (Walker) (Noctuinae) has a brachypterous female but macropterous male (Viette, 1952*b*: 6, pl. 2), whilst both sexes of *D. cunhaensis* Viette (Viette, 1952*b*: 9, pl. 1) are micropterous. Slight wing reduction is also known in the female of *Neoleucania exoul* (Walker) (Hadeninae) whilst its male is macropterous and flies well (Viette, 1952*b*: 14, pl. 3). Microptery, almost certainly in both sexes, is recorded in *Dimorphinoctua goughensis* Fletcher (Fig. 58) (female unknown) (Fletcher, 1963: 17) and *Peridroma goughi* Fletcher (female unknown) (Fletcher, 1963: 18) on South Atlantic Gough Island and *Agrotis patricei* (Viette) (Noctuinae) (Viette, 1959: 25, fig. 5 ♀) on Amsterdam Island in the South Indian Ocean.

An example of brachyptery in the female of an oreal species in Africa is *Saltia acrapex* Tams (Hadeninae) occuring at an altitude of about 4800 m on Kilimanjaro (Tams, 1952: 870, figs 3, 4). The as yet unknown female of the closely related *S. edwardsi* Tams, occurring at an altitude of about 4000 m on Mt. Elgon in Kenya (Tams, 1952: 873, fig. 13, ♂), may also be brachypterous.

In the northern hemisphere wing reduction is observed in the females of certain tundral, oreotundral or oreal Noctuinae. Strong brachyptery is known in *Xestia* (*Schoyenia*) *alaskae* (Grote), north-western Nearctic (Lafontaine *et al.*, 1983: 341, figs 5–7) and *X.* (*S*) *aequeva* (Benjamin),



Figs 54–60 54, *Sattleria basistrigella* (Gelechiidae), Swiss Alps, male. 55, *Sattleria basistrigella* (Gelechiidae), Swiss Alps, female. 56, *Operophtera brumata* (Geometridae: Larentiinae), British Isles (England), mating pair. 57, *Erannis defoliaria* (Geometridae: Ennominae), British Isles (England), female. 58, *Dimorphinoctua goughensis* (Noctuidae: Noctuinae), Gough Island, male. 59, *Pringleophaga marioni* (Tineidae), Prince Edward Islands (Marion Island), male. 60, *Orgyia antiqua* (Lymantriidae), British Isles (England), female.

north-western Nearctic (Lafontaine *et al.*, 1983: 345, figs 8–10), whilst *X.* (*S.*) *brachiptera* (Kononenko), northern Palaearctic (Lafontaine *et al.*, 1983: 347, figs 11, 27, 28) and *X.* (*S.*) *liquidaria* (Eversmann), northern Palaearctic – northwestern Nearctic (Lafontaine *et al.*, 1983: 363, figs 23, 24) are moderately brachypterous and other related species macropterous. Another northern tundral species with moderately brachypterous female is *Xestia* (*Anomogyna*) *laetabilis* (Zetterstedt), Scandinavia – Labrador (Nordström & Wahlgren [1937]: 105, pl. 18, fig. 9, (♂, ♀)).

Moderate to distinct brachyptery has also evolved in the females of several species of the

large genus *Agrotis* Ochsenheimer, including the arcto-alpine *A. fatidica* (Hübner) (Bergmann, 1931: 25, pl. 2; Mentzer & Moberg, 1987: 35, figs 1–4) with its close relative *A. luehri* Mentzer & Moberg from Norway (Mentzer & Moberg, 1987: 40, figs 5–7) and the central Asiatic *A. robusta* Eversmann (Mentzer & Moberg, 1987: 37, fig. 11 (♂)) and *A. trifurcula* Staudinger (Mentzer & Moberg, 1987: 39, figs 9, 10).

According to Dierl & Reichholf (1977: 29) further unspecified noctuine genera with many species, all of them with wing-reduced females and most inhabiting the alpine zone, occur in the high mountain ranges of Asia. However, in spite of an extensive literature search few records were found, e.g. the Tibetan *Perissandria argillacea* (Alpheraki) (Bang-Haas, 1922: 34, pl. 4, fig. 8, as *agama* Staudinger) and *Estimata herrichschaefferi* (Alpheraki) from Siberia and Mongolia. The assumption that the females of all *Estimata* species are wing-reduced (Dierl, 1983: 141) is contentious because that sex is known only in *herrichschaefferi*.

At least two examples of female brachyptery are known in autumn-flying (September-October) central Turkish species of the genus *Victrix* Staudinger (Acronictinae): *V. karsiana lithoxys* Varga & Ronkay (Varga, pers. comm.) and *V. gracilis* (Wagner) (Hacker & Lödl, 1989: 77, pl. 2, figs 1, 2 (♂, ♀)).

Microptery observed in the female of the Mediterranean to western Asiatic *Ulochlaena hirta* (Hübner) (Cuculliinae) (Draudt, 1938: 132, pl. 16 1 (♂,♀)) is interpreted as a result of the cold season effect because the main adult activity period falls into the months October-November (Hacker, 1989: 162). However, this explanation is not entirely satisfactory as there are records of the adults occurring from August onwards. Moreover, *hirta* is restricted to altitudes below 1500 m and inhabits only the warmest spots.

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INDEX

Illustrations are indicated by **bold** page numbers.

Acentropinae 258, 260, 274
Acompsia 268, 270
acrapex, Saltia 280
Acronictinae 258, 280
Adelidae 248
aequeva, Xestia (Schoyenia) 280
agilitata, Sorensenata 249, 260, 270, **271**
Agonoxenidae 263
Agriopis 253, 276
Agrochola 252
Agrotis 245, 282
alaskae, Xestia (Schoyenia) 280
albifemorella, Teleiopsis 268
albitogata, Ethmia 263
allomella, Tinea 259, 263
alluaudi, Xanthorhoe 276
alpicolana, Sphaleroptera 249, 255, 260, **271**
alpina, Lycia 249, 253, 255
Alsophila 250, 253, 275, 276
Alsophiloides 276
alternella, Tortricodes **271**
Alucitidae 244, 252
Alucitoidea 244

amazoula, Epitoxis 280
ampla, Lymantria 278
amuralis, Synaphe 260, 272
Anacampsinae 258, 260, 270
angustispina, Sattleria 260
ankeraria, Erannis 248
anselminae, Pharmacis 258, 261
antiochena, Syntomis 280
antipodensis, Elachista galatheae 259
antiqua, Orgyia 277, **281**
Aoraia 258, 260
apatela, Thyrocopa 246, 249, 250, 251, 255, 259, **264**
Apleria **273**, 276
Apocheima 247, 253, 276
Arctiidae 244, 246, 249, 250, 251, 252, 254, 257, 258, 278
Arctiinae 258
arcuata, Sattleria 260, **269**
Areniscythris 250
argillacea, Perissandria 282
Aristoteliinae 258, 259, 268
Asaphodes 251, 274, 276
atlantis, Ceuthomadarus 260
Atomotricha 252
attenuata, Campbellana 249, 260, 263, 272
aucklandica, Tinearupa sorenseni 259
aurifluella, Ethmia 247
auronitens, Deuterotinea 258
avellanella, Semioscopis 252
axiurga, Deuterotinea 258

baetica, Ocnogyna 279
balcanica, Deuterotinea 258
banghaasi, Elophos 276
barnsi, Xanthorhoe 276
basalis, Orgyia 277
basistrigella, Sattleria 260, **281**
Batrachedrinae 263
bertrandi, Pharmacis 258
biformella, Catoptria 260, 273
binotellus, Megacraspedus 259
Biston 247
Bistonini 258, 274
blandiata, Perizoma 247
Blastobasidae 254, 255, 258, 259, 265
blattariella, Anacampsis 268
bodillum, Gnorimoschema 249, 268
bombycalis, Synaphe 260, 272
Bombycoidea 258, 276
Borkhausenia 244, 251
Bracharoa 278
brachiptera, Xestia (Schoyenia) 281
brachyptera, Ambloma 251, 259, 265, **266**, 268
brachyptera, Eudarcia 259, **261**, 263
brachypterella, Biselachista 259, 265, **266**
brachypteris, Areniscythris 246, 249, 250, 252, 260, 268, 270
bretaudiaui, Spilosoma 280
breveti, Maurica 279
breviramus, Sattleria 260
brittoni, Paracles 280
bruceata, Operophtera 254
brumata, Operophtera 253, 254, **281**
byrsopola, Proterodesma 262

caelibaria, Elophos **275**, 276
calliceros, Pollanisus 260, **271**, 272
Calliduloidea 244
campbellensis, Asaphodes 274
Carposinidae 258, 260, 272
Caryocolum 245, 268, 269
casanella, Deuterotinea 258, 260
Castnioidea 244
Catoptria 245, 248
Ceuthomadarus 244, 270
charybdis, Ethmia 247, 259, 263
Cheimophila 244, 265
Cheimoptena 276
Chimabachinae 252, 258, 259, 265
Chionodes 268
chloronota, Atomotricha 259
Chondrosoma 276
Chondrostega 245, 256, 277
cinerella, Acompsia 268
clarkei, Proteodes 259
clathrata, Semiothisa 247
Coleophoridae 244, 263
congelatella, Exapate 249, 260, 270, **271**
Copromorphoidea 249, 258, 272
Coscinia 279
Cosmopterigidae 258, 259, 267
Cossoidea 244
Crambinae 258, 260, 273
crenaeus, Orocrambus 260, 274
crozetensis, Pringleophaga 259
Ctenuchinae 244, 258, 278, 280
Culculliinae 258, 280
culex, Diptilon 244, 278
culminicola, Megacraspedus 259, 268
cunhaensis, Dimorphinoctua 250, 280
cupreifera, Diurnea 259
curtipennis, Ephysteris 251, 259, 269
Cymbalophora 280

Daltopora 268
defoliaria, Erannis 245, 246, 250, **281**
Depressariinae 252, 258, 259
Descoreba 276
deserticola, Paracles 280
detectendum, Paraschema 259
detersa, Lymantria 278
Deuterotinea 262
digitella, Catoptria 260, 273
dimorpha, Acompsia 249, 255, 260, **269**, 270
dionysias, Asaphodes 276
discrepitella, Ethmia 259, 263
dispar, Lymantria 245, 277
Diurnea 244, 249, 250, 265
dolosellus, Megacraspedus 259, **266**
dregei, Bracharoa 278
dubia, Orgyia 246, 277
duratella, Exapate 248, 253, 260, 270
dzieduszyckii, Sattleria 260

edwardsi, Saltia 280
Elachista 244, 248, 251, 265
Elachistidae 258, 259, 265
elbursicum, Gnorimoschema 259, 268
electilis, Kupea 260, 274
Elophos 245, 276
Ennominae 252, 258, 274
ephemeraeformis, Thyridopteryx 249
ephemerella, Acentria 256, 260, 274
Ephysteris 245, 248, 251, 255, 259, 268, 269
Erannis 250, 252, 253, 275, 276
ericae, Orgyia 246, 277
erichrysa, Metacrias 280
Eriocottidae 252, 258, 262
Eriogaster 277
Estimata 245, 282
Ethmia 244, 247
Ethmiinae 252, 258, 259, 263
Eudarcia 244, 263
Eulamprotes 268
Eurota 280
eversmanni, Lasiocampa 277
exiguana, Oxypteron 260, 272
exoul, Neoleucania 280
extremella, Vulcaniella 259, 267

fagella, Diurnea 250, 259, **264**
falklandensis, Borkhausenia 259, 265
falklandicellus, Fernandocrambus 273
fatidica, Agrotis 250, 255, 280, 282
felixi, Daltopora 259, 268
fiduciarium, Chondrosoma 253, **275**, 276
fugacella, Teleiodes 267
fugitivella, Teleiodes 267
fumida, Cheimophila 259
funebrella, Ceuthomadarus 260, 270
fusca, Pygmaena 275, 276

galatheae, Elachista 249, 259
gallica, Eudarcia 259, 263
Gelechiidae 252, 254, 258, 259, 267
Gelechiinae 258, 259, 267, 268
Gelechioidea 249, 258, 263
Geometridae 244, 246, 247, 248, 249, 252, 253, 254, 256, 258, 274
Geometroidea 258, 274
geranella, Ethmia 263
glaucoterma, Kiwaia 259, 269
Glyphipterigidae 258, 263
Gnophini 258, 274
Gnorimoschema 268
Gnorimoschemini 258, 259, 267, 268
goughensis, Dimorphinoctua 280, **281**
goughi, Peridroma 280
grabowiella, Vulcaniella 267
gracilis, Victrix 282
Gracillariidae 244, 252
graminea, Exsilirarcha 248, 249, 250, 251, 260, **273**, 274
groenlandica, Gynaephora 277
gutierreziae, Synalocha 271

Hadeninae 258, 280
hageni, Udea 260, **273**, 274
halticella, Embryonopsis 248, 259, 263
haroldi, Cymbalophora **279**
hastata, Eulype 247
hecta, Phymatopus 261
Hedyloidea 244
Heliconius 257
Hemerocampa 277
Hepialidae 244, 247, 248, 254, 258, 260
Hepialoidea 258, 260
herrichschaefferi, Estimata 282
Hesperioidea 244
heterogyna, Laelia 278
Heterogynidae 246, 249, 250, 251, 258, 260, 272
Heterogynis 260, 272
heterospila, Nomophila 274
hiemalis, Dasyethmia 253, 259, 264

hirta, Ulochlaena 250, 282
Holcopogonidae 263
holdgatei, Elachista 259
homsana, Oxypteron 260, 272
hookeri, Elachista 259
hopkinsi, Orgyia 277
humuli, Hepialus 261
huttoni, Metacrias 280

ilicis, Trichiura 277
imitatrix, Paracles 280
Immoidea 244
impar, Oxypteron 260, 271, 272
imparellus, Megacraspedus 259
incerta, Lymantria 278
indocilisaria, Zermizinga 252, 276
innocuella, Anacampsis 268
insipida, Paracles 280
inspersella, Scythris 249, 270
instabilis, Deuterotinea 258
Inurois 276
isogama, Atomotricha 265
issikii, Diurnea 259
Itame 276
iveni, Elophos 276

Janseola 272
jeanae, Kiwaia 249, 259, **267**, 269

kasyi, Ephysteris 260, 269
kerguelensis, Pringleophaga 259
Kessleria 244, 255, 259, **261**, 263
kindermannaria, Spartopteryx 244, **275**
Kiwaia 245, 268
klimeschi, Ambloma 265
kurentzovi, Cheimophila 259

laceratella, Caryocolum 249, 255, 260, **267**, 270
ladakensis, Lachana 278
laetabilis, Xestia (Anomogyna) 281
Lambessa 256
lanceolellus, Megacraspedus 259
lanestris, Eriogaster 252
Larentiinae 252, 258, 274
Lararannis 275
Lasiocampa 256, 277
Lasiocampidae 247, 250, 252, 257, 258, 276
Lecithoceridae 248, 254, 258, 260, 270
lectus, Orocrambus 273
libanotica, Syntomis 280
libertinella, Eulamprotes 259, **267**, 268
libyssa, Coscinia 279
lindsayi, Orocrambus 260, 274
lineatonotella, Ethmia 247
liouvillei, Coscinia libyssa 279
Lipteninae 246
liquidaria, Xestia (Schoyenia) 281
Lithosiinae 258, 278
lithoxys, Victrix karsiana 282
loricaria, Itame 276
luehri, Agrotis 282
lugens, Gynaephora 278
Lycaenidae 246
Lycia 247, 276
Lymantria 278
Lymantriidae 246, 247, 248, 249, 250, 251, 256, 257, 258, 277
lynosyrana, Synnoma 253, 260, 271
Lyonetiidae 252

macelhosiella, Ethmia 263
maculosella, Acompsia 270
majorella, Catoptria 260, 273
maracandica, Deuterotinea 258
marginella, Pleurota 245, 246, 248, 249, 259, **264**, 265
marioni, Pringleophaga 259, **281**
mediomaculata, Thyrocopa 264
Megacraspedus 248, 265, 268
melaleucella, Sattleria 249, 260
melanoleuca, Aroa 278
mestralii, Syntomis **279**, 280
Metacrias 280
meteus, Automolis 280
microphthalma, Tinea 256
Micropterigidae 248
Mimallonoidea 244
moldavica, Synaphe 260, 272
Momphidae 252, 263
mongolica, Stomopteryx 260, 270
monolorellus, Megacraspedus 259
montana, Mesocelis 277
morio, Penthophera 278

naumanni, Ceuthomadarus 260, 270
nephelias, Asaphodes 276
Nepticulidae 244
Noctuidae 246, 252, 253, 254, 258, 280
Noctuinae 258, 280
Noctuoidea 258, 277
Nymphalidae 252
Nymphulinae 256

obfuscata, Lymantria 278
ochrogastra, Chersadaula 259, 265
Ocnogyna 250, 253, 256, 278, 279
oculatalis, Synaphe 260, 272
oculella, Semioscopis 252, 253
oeconoma, Atomotricha 259, 265
Oecophoridae 248, 252, 256, 258, 259, 263
Oecophorinae 258, 259, 265
Oenochrominae 252, 258, 274
Olethreutinae 258, 260, 270
ommatias, Atomotricha 249, 259
Operophtera 250, 253, 275, 276
Operophterini 258, 274
Opostegidae 252
orestera, Olethreutes 260, 271
Orgyia 245, 249, 250, 277
Orocrambus 245, 273
Orthosia 252
oxyptera, Asaphodes 274
Oxypteron 245, 271

Pachyligia 276
palaestinensis, Deuterotinea 258
Papilionoidea 244
Paracles 280
paradoxella, Deuterotinea 259, 262
parasita, Ocnogyna **279**
pardalina, Tancrea 279
patricei, Agrotis 280
penella, Heterogynis 250, 272
pennigera, Cheimoptena 245, 246, 252, 253, 275, 276
pergrandella, Chionodes 245
Peridroma 251
Phaos 280
Pharmacis 244, 248, 261
phryganella, Diurnea 259
Pieridae 252, 257
pilifera, Dimorphinoctua 280
pityocampa, Thaumetopoea 246
plagiobothrae, Ethmia 263
plemochoa, Kiwaia 259, 268
Pleurota 244, 265
Poecilocampa 277
poliella, Agriphila 273
pometaria, Alsophila 254
pomonaria, Lycia 255
pomposella, Vulcaniella 267
populella, Anacampsis 268
populi, Poecilocampa 252
powelli, Maurica breveti 279
Pringleophaga 248, 262
Procridinae 258, 260
profanella, Symmoca 259, 266
Protalcis 252, 275
provincialis, Synaphe bombycalis **273**
Psychidae 246, 247, 248, 249, 250, 251, 256, 258, 259, 262
Pterolonchidae 263
Pterophoridae 244, 252
Pterophoroidea 244
pudens, Ocnogyna 279
pumila, Dasorgyia 278
pumila, Elachista 259
punctalis, Synaphe 260, 272
Pyralidae 252, 254, 256, 258, 260, 272
Pyralinae 258, 260, 272
Pyraloidea 249, 258, 272
pyrausta, Ethmia 263
Pyraustinae 258, 260, 274
pyrenaica, Kessleria 259
pyrenaica, Sattleria 260, **269**
pyrenaicus, Pharmacis 255, 258, **261**

quadripunctaria, Alsophila 248

reductus, Crambus 260
regraguii, Stoermeria 277
rhombelliformis, Gelechia 268
rivularis, Cymbalophora 279
robusta, Agrotis 282
rossii, Gynaephora 277, 278
rotundata, Iropoca 278
rudis, Paracles 280
rugata, Glyphipterix 259, 263
rungsi, Ceuthomadarus 260

salicella, Cheimophila 253, 259
Sattleria 245, 246, 249, 250, 255, 268, 269
Saturniidae 257
Sauris 244, 275
scaphodes, Protyparcha 260, 274
Schrankia 256
Scopariinae 258, 260, 274
Scrobipalpula 249, 268
Scythrididae 250, 258, 260, 270
Scythris 250
selenophora, Dasorgyia 278
Semiothisini 258, 274
senex, Aoraia 258, 260
separatellus, Megacraspedus 259
serrula, Lasiocampa 277
Sesioidea 244
Setina 251, 278
signella, Symmoca 259, **266**, 267
socialis, Eucheira 257
soljanikovi, Diurnea 259

Somabrachyidae 252, 258, 260, 272
Somabrachys 256, 260, 272
sordida, Atomotricha 259
sorenseni, Tinearupa 259, 263, 265
spegazzinii, Eurota 280
Sphingidae 253
Sphingoidea 244
staudingeri, Lasiocampa 277
Stomopteryx 245, 268, 269
strategica, Metacrias 280
strigiventris, Eurota 280
stschetkini, Deuterotinea 258, 262
styriaca, Sattleria 260
subdolellus, Megacraspedus 259
superbella, Eulamprotes 268
Symmoca 245
Symmocidae 248, 254, 258, 259, 265
Synaphe 245, 272
Syntomis 280
syriaca, Pararhodobates 259, 262

tasmanica, Thermeola 278
Tatosoma 275
Tegenocharis 260, **269**, 270
Teia 277
tenebraria, Sciadia 276
thyellina, Orgyia 278
Thyretinae 278, 280
Thyrocopa 244, 246, 250, 264
Tinea 244
Tineidae 248, 252, 254, 256, 258, 259, 262
Tineinae 256
Tineoidea 258, 262
Tortricidae 252, 254, 256, 258, 260, 270
Tortricinae 258, 260, 270
Tortricoidea 249, 258, 270
Trichiura 277
trifurcula, Agrotis 282
tripunctella, Acompsia 268, 270
turbotti, Proterodesma 259, 262
turneri, Lymantria 278
turpella, Gelechia 268
Tympanota 244, 275

Udea 251

vallantini, Lemonia 252
versuta, Atomotricha 259
viciella, Megalophanes 249
Victrix 282
viduellus, Ceuthomadarus 260
villosa, Aponotoreas 276
Vulcaniella 267

wellsi, Xanthorhoe 276
wilkella, Eulamprotes 268

Xanthodule 278
Xanthorhoe 245, 276
Xanthorhoini 274
Xestia 245
Xyloryctinae 258, 259, 264

Yponomeutidae 252, 254, 258, 259, 263
Yponomeutoidea 249, 258, 263

zelleraria, Elophos 275, 276
zimmermanni, Kessleria 249, 259
zirbitzensis, Elophos 276
zonaria, Lycia 253, 255, 276
zoraida, Ocnogyna 279
Zygaenidae 244, 258, 260, 272
Zygaenoidea 258, 272

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CONTENTS

205 ***Sattleria*: a European genus of brachypterous alpine moths (Lepidoptera: Gelechiidae)**
Linda M. Pitkin & K. Sattler
243 **A review of wing reduction in Lepidoptera**
K. Sattler

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